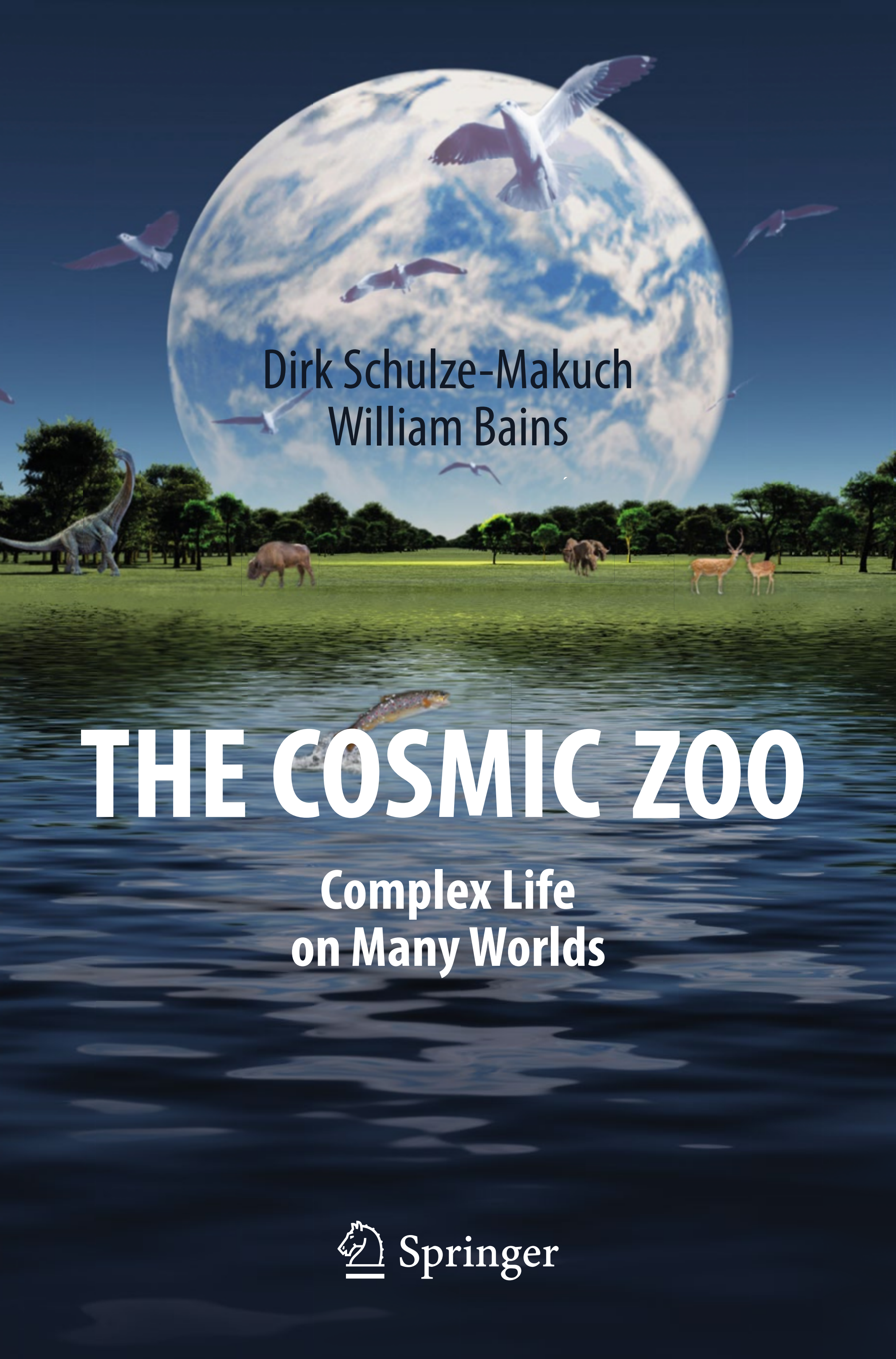

Dirk Schulze-Makuch
William Bains

THE COSMIC ZOO

Complex Life on Many Worlds

Springer

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Dirk Schulze-Makuch • William Bains

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Dirk Schulze-Makuch
Center for Astronomy and
Astrophysics (ZAA)
Technical University Berlin
Berlin, Germany

William Bains
Rufus Scientific Ltd.
Melbourn, Royston
United Kingdom

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Preface

One of our most persistent questions is whether we are alone in the Universe. We now know that the sky is full of planets, but are they empty, sterile worlds, worlds harbouring only simple, primitive life, or is there a good chance that there are thinking, talking, machine-making creatures out there for us to talk to? Science is starting to provide the tools to answer that question. In this book, we will discuss what we know about the steps that lead from the origin of life on Earth to ourselves, using an approach that allows us to ask whether humanity is a galactic oddity, or whether complex, smart, and potentially technological beings are highly likely to evolve on an Earth-like planet in the 10 billion years available to it between the condensations of the oceans on the planet's surface and their evaporation by the increasing radiation from the Sun.

There are probably as many opinions on this subject as there are scientists. This book represents our synthesis of the facts and opinions and our explanation why we think complex life may be common. Here, we lay out how we understand the evolutionary pathway from the origin of life to us humans, and what this means for life that we think exists elsewhere in the Universe, and why we think that smart, tool-making creatures may arise on other worlds, maybe on many other worlds. There are some steps on the ladder to complexity which we feel more confident about than others. We will point out the weaker steps as we discuss them, but overall we feel that the argument is compelling.

We thank Frances Westall, Charles Cockell, and an anonymous reviewer for their constructive comments, and Louis Irwin for frequent and fruitful

discussions, which improved the book significantly, and our editor Christian Caron for guiding us along this book project. We are also grateful to our families, particularly our wives, Joanna Schulze-Makuch and Jane Bains, who had to put up with us while we were even more preoccupied than usual while writing this book.

Berlin, Germany Dirk Schulze-Makuch
Melbourn, Royston, UK William Bains

Introduction

Is there intelligent life other than humans in the Universe? It is an ancient question. We still can't answer this question, but based on new scientific insights we can speculate on what the answer may be. This book is based on what we know of life on Earth, and what that can tell us about how likely it is that complex, active, tool-using life could evolve elsewhere.

Unlike many books on life in the Universe, we are not much concerned with bacteria or algae except in that they illuminate the path to us. We happily admit that this is a highly anthropocentric approach, but we take it deliberately because we are interested in the evolution of complex, smart organisms. We look into the night sky and see no aliens, and so we ask, with Enrico Fermi, 'If life is so common, where are they?' This is a paradox. It is widely believed that life will arise on any suitable planet (although we will question this in Part II). Yet, we see no examples of intelligent, radio-transmitting, spaceship-making life in the sky. So there must be what Robin Hanson calls 'The Great Filter' between the existence of planets and the occurrence of a technological civilisation. That filter could, in principle, be any of the many steps that have led to modern humanity over roughly the last 4 billion years. So which of those major steps or transitions are highly likely and which are unlikely? What implications does this have for the likely frequency of life, particularly complex and technologically advanced life?

To answer this, we can identify features of our current biology that are central to our existence and nature, such as having bones or brains, and those that are peripheral, such as possession of earlobes, and seek to find the point in our evolution where the key features were acquired. We are not arguing for similarity in appearance, or what we will here parody as The Star Trek

Fallacy—that it is inevitable that complex, intelligent aliens will all have pentadactyl limbs, circular irises, and male-restricted facial hair. With Stephen J. Gould, we agree that rewinding and replaying the tape of life on Earth (or playing it again on a comparable planetary body) will not result in humans. Here, we are concerned with the processes that result in *function*, not specific anatomy. For example, the vertebrate eye is specific and perhaps unique, but vision has evolved many times, producing the completely different eyes of insects, spiders, molluscs, cephalopods, trilobites, and, of course mammals. We are less concerned with how a creature is smart and more whether it is smart.

Progression of life from the earliest forms to ourselves is often characterised as a series of major steps, transitions, or key innovations, each providing a significant new capability to the newly evolved organisms that was lacking in more primitive forms. Evolution does not occur linearly with a goal in mind (there is no 'mind'!). Each evolutionary step adds a new toolset to solve environmental challenges that each life form stumbles on, based on anatomical, biochemical, and genetic abilities that are already there. So what are the key steps or innovations and where do they occur on the path from the Last Universal Common Ancestor to humans? Which of the major key innovations from the origin of life to a technologically advanced society like ours are highly likely and which are unlikely? Where does the 'Great Filter' lie?

This book is trying to provide some answers. The title gives our answer away—we think that once life has arisen on a world, complex life is highly likely to evolve. If life is common, we believe that we live in a Cosmic Zoo.

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Part I

The Cosmic Zoo Hypothesis

1

The Cosmic Zoo Hypothesis and the Evolutionary Tool Set

In this book, we will argue that the evolution of complex life is highly likely in any stable, sufficiently extensive environment once life originated on a planetary body.

Complex life on Earth are the true (obligate) multicellular lifeforms, particularly members of the kingdoms Plantae (plants), Fungi (the yeasts and funguses) and Animalia (animals) (Box 1.1). Being made of many, specialist cells is the hallmark of this sort of advanced, complex life. If stable habitable rocky planets are rare, then complex life is rare in the Universe. If the origin of life on those planets is extremely rare, then life is very rare and we live in a rather *Empty Universe*. However, if the origin of life is common and habitable rocky planets are abundant then life is common, and we live in a *Cosmic Zoo*. Recent research successes in the detection of exoplanets seem strongly to indicate that rocky planets are common. Not all are suitable for complex life. Some cannot support life at all. Some may only be able to support simple life; complex life needs a large habitable volume, and there has to be a lot of life on the planet (technically, a large total biomass). The environment has to be stable (although environmental parameters such as temperature might not have to be as tightly constrained for complex life as we observe it from Earth). But within these cosmic constraints, our hypothesis is that all major transitions or key innovations of life toward higher complexity will be achieved by a sufficient large biosphere in a semi-stable habitat given enough time.

There are only two transitions of which we have little insight and much speculation—the origin of life itself, and the origin (or survival) of technological intelligence. Either one of these could explain the Fermi Paradox—why we

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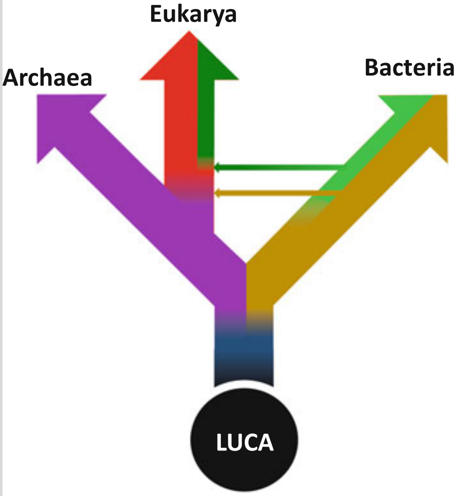
have not discovered (yet) any sign of technologically advanced life in the Universe. The final test of our hypothesis will be when our space faring and remote sensing abilities allow us to explore other planets and moons beyond our Solar System and detect possible biospheres on them, which would be one of the grandest achievements of our species.

Box 1.1 Major Branches of Life

All life on Earth shares a common chemical basis, and so is believed to have evolved from a common ancestor, called the Last Common Ancestor (LCA) or sometimes the Last Universal Common Ancestor (LUCA).



The LCA or LUCA probably dates from near the origin of life, but we do not know for sure. The LCA may not have been alone on the Earth, but we have not found any descendents of other life-forms from that era. The LCA was a relatively simple unicellular organism. Its descendents evolved into two different groups, the archaea and the eubacteria (often just called 'bacteria'). One group of archaea were probably the ancestors of the third group of organisms, the eukaryotes—organisms whose cells have nuclei and mitochondria or their derivatives. Close to or at the origin of the eukaryotes the ancestoral cell engulfed an alphaproteobacterium (brown left arrow), which became the mitochondria. One group of bacteria evolved the capability of using the Sun's light to capture CO_2 and produce oxygen as waste—these were the ancestors of the cyanobacteria (green). One of these was captured by a eukaryote (green left arrow) and formed the ancestor of the chloroplast in today's green plants. Note that many of the transitions are not well-defined steps—we do not know the order or timing of many of these events.

1.1 Modeling the Transitions of Life

After roughly 4 billion years of evolution, one species (us) that is intelligent and that uses technology has appeared. The evolution of complex animal life on Earth is the result of a number of major steps at which life has acquired new capabilities, and several of these steps or major transitions have been identified. These major transitions have occurred spread out over geological time and were linked to the specific environmental conditions that the life form was exposed to. Our goal is to explore how probable each of these key innovations is, and hence how likely it is that the same transition might occur on other worlds.

To do this, we have a simple approach. We suggest that there are three classes of explanations for a major transition or key innovation in the history of life, based simply on how they occur:

1. The Critical Path Model. Each transition requires preconditions that take time to develop. However the time is (at least mostly) determined by the transition and the underlying nature of the planet, and so once the necessary preconditions exist on the planet then the transition will occur in a well-defined timescale. It is like filling up a bath tub; once you turn on the taps, the bath will fill up. It just takes time.
2. The Random Walk Model. Each transition is highly unlikely to occur in a specific time step, and the likelihood does not change (substantially) with time. This may be because the event requires a highly improbable event to occur, or a number of highly improbably steps. So substantial time has to elapse before the transition occurs by chance. Once life exists on a planet, ultimately the key innovation will occur, but when it occurs is up to chance, and whether it occurs before the planet runs out of time and becomes uninhabitable is not knowable. It is like having to throw a certain number of 6s in a row with a dice; it may or may not happen in the allowed time.
3. The Many Paths Model. Each transition or key innovation requires many random events to create a complex new function, but many combinations of these can generate the same *functional* output, even though the genetic or anatomical details of the different outputs are *not* the same. So once life exists the chance that the transition will occur in a given time period is high, but the exact time is not knowable. It is like getting a good hand in poker; the chance of getting a particular hand is tiny, but there are many different ‘good’ hands, and you can be confident that you will get one every now and again.

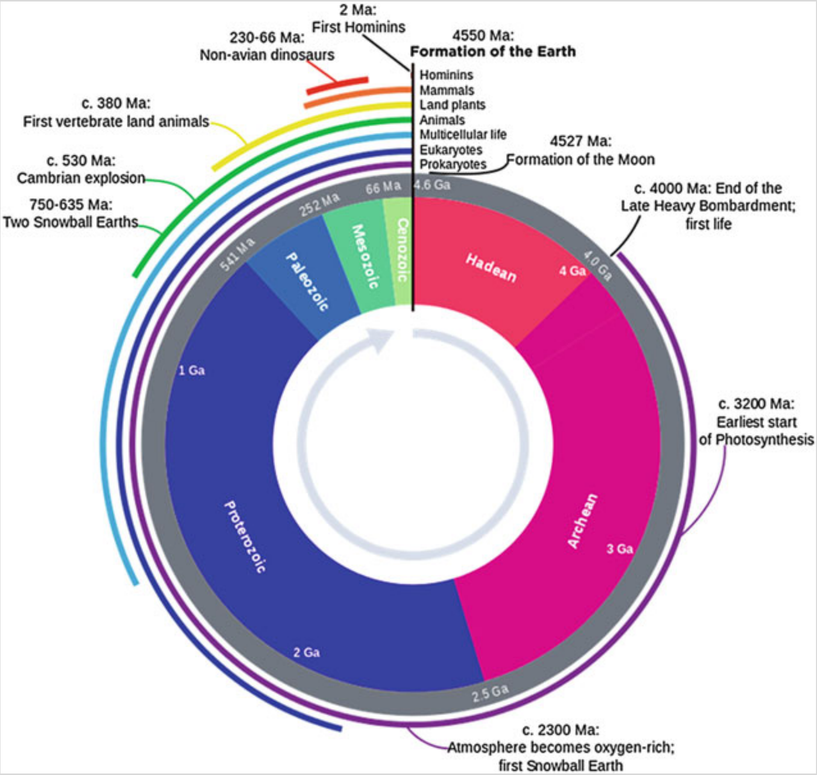
Each of these may also fall into a fourth category, which we name a Pulling Up The Ladder Event. In this class of explanation, an innovation is likely (either because it is a Critical Path or a Many Paths process), but the results of the innovation destroy the preconditions for its own occurrence. The new organisms “pull up the ladder after themselves”. We argue that the major transitions of life can be explained with this tool set to a large degree.

An example of the Critical Path model might be one of the explanations given for the appearance of diverse hard-shelled animals on the Earth about 541 million years ago, commonly referred to as the Cambrian Explosion. The argument (which we will return to in Chap. 9), says that animals need oxygen to help power their high-energy metabolism. The bacterial precursors of plants had been making oxygen for over a billion years before animals appeared. But all that oxygen was consumed by the rocks on the surface of the Earth and volcanic gases coming from its interior through volcanoes. Only when those rocks were all completely oxidized and could absorb no more oxygen could oxygen gas start to build up in the atmosphere. Thus a long time had to pass between the evolution of oxygen-producing photosynthesis and the appearance of animal life. Once oxygenic photosynthesis had appeared, the appearance of animals was highly likely, but only after a long delay.

An example of the Random Walk Model might be the argument that mammals became the dominant large animals on Earth because of two preconditions; the evolution of early, small mammals and the availability of ecological niches into which they could evolve to become the large, diverse animals we see today. Early mammals had been on the Earth since the Triassic period (Box 1.2), but the ecological niches for large herbivores, and the large carnivores that ate them, were filled by the dinosaurs. Mammals remained small and nocturnal. Then a random event happened which opened up that niche for the mammals; a comet or asteroid collided with the Earth near what is today the town of Chicxulub in Mexico at the end of the Cretaceous, which combined with prior climate change, wiped out the dinosaurs, and opened up the ecological niches for mammals to evolve into. That impact could have happened at the end of the Jurassic, or during the Eocene, or could not have happened yet. If it had not happened at all, then the mammals might today still be the rare, small, nocturnal animals they were 70 million years ago.

An example of the Many Path Model is the evolution of imaging vision. Eyes that can make images of the world (not just detect light and dark) have evolved many times in insects, cephalopods, vertebrates, and extinct groups like the trilobites. They evolved independently, and all have different structures, as a comparison of insect and human eyes will instantly show. But all these different, independently evolved eyes perform the same *function.*

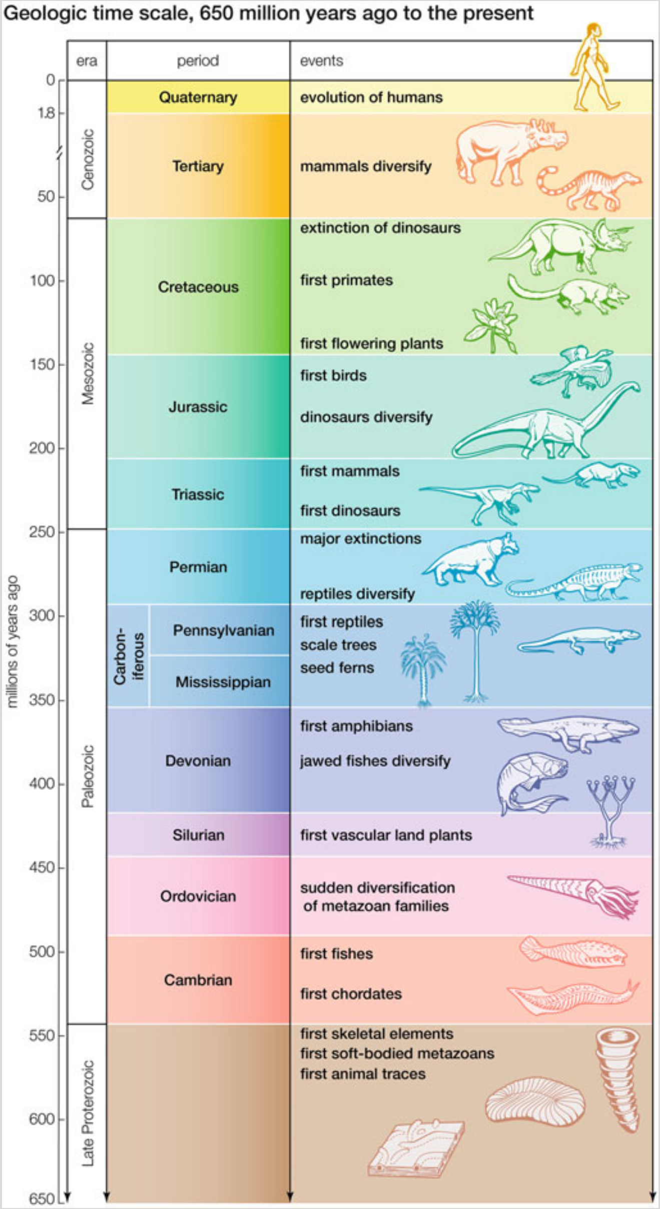
Box 1.2 Geological Time Scale from the Origin of Earth Until Today



Clock representation showing some of the major highlights of the natural history of Earth (above). Note that the time of the first humans is too small to fit into the scale. Highlighted below are the last 650 million years of natural history, with the major geological time periods and events in the history of life, starting with the approximate arrival of the first animals. Absolute age assignments are uncertain and many of these are controversial, for both figures.

(continued)

Box 1.2 (continued)



A geologic time scale showing major evolutionary events from 650 million years ago to the present. Credit: Encyclopaedia Britannica/UIG/Getty Images.

We classify innovations in this way because this tells us something about *timing* and *probability*, which is what we want to know, without us having to worry about *mechanism* (for example, exactly which genes are involved in building an insect or a vertebrate eye, and how they evolved). Remember that we are concerned here with the evolution of a *function* (e.g. imaging vision), and not a *structure* (e.g. an eye with a lens and a retina, like our eyes).

1. Critical Path Model. For this, you only need one set of preconditions to be true. Once those preconditions are in place, the innovation will arise in a defined time, and will occur on all occasions that the preconditions happen. The preconditions only take time, there is not a major role for chance. The time might be very long (as is the case on the proposed link between oxygen and animal life above), but it is predictable if you know enough about the planet and its biosphere. If an innovation occurs through a Critical Path process more than once, it will probably follow a similar evolutionary path in the different examples, and so independent evolution of the function will come from similar mechanisms or structures.
2. Random Walk Model. There are no particular, specific preconditions needed, other than the existence of life that can achieve the innovation (for example, vision is unlikely to evolve in an environment where there is no light to see). So the innovation will occur at random. Because by definition it is quite unlikely to occur—if it was likely, it would occur easily and would not be a key innovation or major transition—then it is unlikely to occur twice.
3. Many Paths Model. There are no specific preconditions for a Many Paths process other that prior existence of life that can achieve the innovation. However, once any appropriate precondition is met, the innovation will happen fairly reliably some time afterwards (as measured in generations). So it is almost inevitable that the innovation will occur eventually. But because there are many ways that it can occur, then each time the *function* will be carried out by a different *mechanism.*

A Many Paths process is not the same as a Random Walk process. In the Random Walk process, many events have to occur, but when they occur is random—the result is that the timing of the overall event is random. By contrast, in the Many Paths process, many combinations of random events can cause an event or innovation. A curious result of the math is that the timing of the overall event is more predictable than the timing of any of its component, individual (random) events. This is a commonplace in everyday life. The owner of a fast-food restaurant cannot predict when a particular customer will come in to order a burger, but he can predict at the end of the day the number of burgers sold, and thus order appropriately in advance. The Many Paths model argues that if an event can be caused by many combinations of random events, then it will inevitably happen, and it will have a high probability of happening in a defined time period.

So we can discriminate between the three models, illustrated in Fig. 1.1. If a major innovation has occurred only once, we might favour the Random Walk Model. If it occurred many times spread through evolutionary time, we may prefer the Many Paths Model. If it occurs many times with a very diverse set of

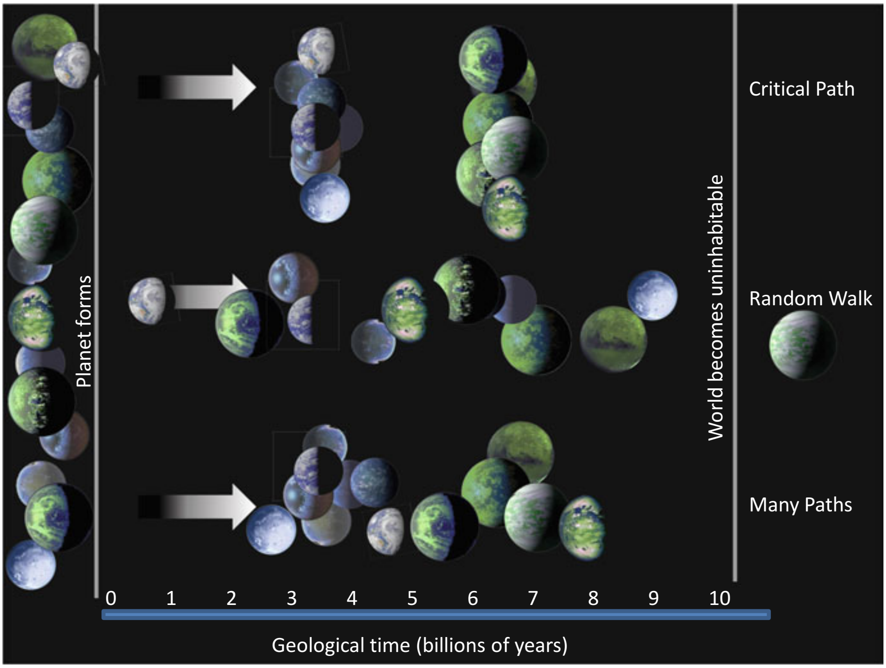

Planet forms
Critical Path
Random Walk
Many Paths
World becomes uninhabitable
0
1
2
3
4
5
6
7
8
9
10
Geological time (billions of years)

Fig. 1.1 Timing implications of the three evolution models (schematic). Here we illustrate the three models with just two types of worlds—an Earth-like planet (*blue*) and a dryer Super-Earth (*green*). The Critical Path model predicts that a particular transition will happen at more-or-less the same time on all worlds, given the same characteristics of that world. Here, on the *blue*, Earth-like worlds that transition happens at 3.2 billion years after planet formation, on the *green* Super-Earth worlds it happens later at 6.5 billion years. The Random Walk model predicts that it could happen any time, and on some worlds it does not happen before the world becomes uninhabitable (here at 10 billion years). The Many Paths model predicts that the transition will happen within a fairly constrained band of time, again depending on when the planet achieves the preconditions necessary for the transition, which here is 3.5 billion years for the *blue* worlds and 6.5 billion years for the *green* worlds. Planet images derived from images courtesy of NASA

mechanisms, we are even more confident that the Many Paths Model is the appropriate way to describe how the key innovation was achieved. If it occurred many times but very close together in the geological record, we might think it is a Critical Path process. Even if we do not know when it evolved, but see that a function evolves several times independently and uses the same mechanism each time (for example the same set of genes or the same basic anatomical structure) then again we might favour the Critical Path model.

We came up with these three types of explanation so that we can try to answer our original question. Clearly, humans are unique. We only evolved once, the chance of evolving something just like a human is astronomically small, and the evolutionary path to humans is vastly complicated and mostly unknown. But we are not concerned with whether humans evolve elsewhere. We want to know whether tool-using, smart, dynamic organisms evolve elsewhere, and that is about the evolution of *function* rather than *anatomy.* Our models allow us to separate the likelihood that a function evolves from both the specific evolutionary path it took to evolve, and from the anatomy or biochemistry of the final organism. We can ask "How often does vision evolve?" and not get lost in the maze of specific genes and cells that make up the human or the insect eye.

This distinction between structure and function is central, and so we will give just one more example. The placenta (the 'afterbirth') was thought to be unique to mammals. It allows the mother to feed the baby in the uterus, allowing the fetus to grow to quite an advanced state while being protected by the mother from everything from viruses to tigers. The mammalian placenta is indeed unique. It has a specific anatomy that is found in no other group of animals. But its function is not unique. The function of the placenta is to bring the mother's tissue and the fetus's blood supply close enough to allow nutrients to pass easily from mother to fetus inside the mother's body. If we ask whether other animals have evolved specialist tissue or organs to carry out this function, then the answer is definitely yes; scorpions, some species of cockroaches, some lizards, sharks and snakes have their maternal and embryonic tissue arranged in specific tissue to allow the growing fetus to gets its oxygen and nutrients from its mother. Some of these viviparous animals (for example placental reptiles) allow the fetal tissue to contact the mother's blood directly, something that until recently was thought to be a uniquely mammalian feature. Vivipary has evolved many times, independently, with different anatomy giving the same function each time. Far from being a unique, improbable, Random Walk feature of mammals, the evolution of vivipary is a Many Paths process that has occurred in a wide range of animal groups.

So we can separate how likely a function is to arise from the details of how that function happens if we have some examples to study.

In this book we are concerned with major steps in evolution, and hence the emergence of radical, biosphere-changing functions. In Part II of this book we will analyze those major transitions or key innovations of life, to ask whether they follow a Critical Path Model, a Random Walk Model, or a Many Paths Model. Based on these analyses we can then judge how readily each major transition can be conquered by life (Fig. 1.1). Is Earth an exceptional and unusual place for life in the cosmic neighborhood as has been argued by Peter Ward and Donald Brownlee in their book *Rare Earth*? Or, do our results imply that we are living in a *Cosmic Zoo*? But before we are getting to this question, we have to take a look of what the planetary conditions have to be in order to allow the evolution of complex, macroscopic life.

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2

Pre-conditions for Complex Life

Before we start to discuss how life evolves on a planet, we have to address whether a planet can support life even in principle. The minimum requirements are at a higher bar for complex life than for microbial life. We will start our discussion by reviewing what makes Earth a habitable planet, and how our planetary history is closely interwoven with the rise and persistence of life, in stark contrast to our neighboring planets which seem rather inhospitable. Then we discuss the astronomical and planetary constraints on habitability and life, particularly complex life, and speculate whether the preconditions for life are common in the Universe.

2.1 A Very Brief History of Earth and Life Through Time

Earth is thought to have formed with the other bodies in the Solar System about 4.54 billion years ago by a process of accretion. The whole solar system formed from a cloud of dust and gas, which collapsed under its own gravity to a spinning disc called the protoplanetary disc. The gas and dust aggregated into a range of larger bodies in this disc. The largest of these was of course in the center, and became our Sun, but many others formed in orbit around the Proto-Sun. These small bodies, called planetisimals were similar to today's asteroids and comets. There were millions of them, and they also collided with each other, building up larger bodies that became protoplanets, large enough

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for their gravity to attract more comets, rocks and dust. Glancing blows gave the growing planets their rotation. Near to the Sun chemicals like water and methane were warmed up to form gas; there protoplanets were mostly made of the rock left behind when the gas evaporated. These bodies became the inner terrestrial planets of our Solar System. Further from the Sun water, ammonia and methane were frozen as solid particles, and these also stuck to the planetisimals. Those planetary bodies would gather up ices, gases as well as dust. They grew fast, and today became the large gas giant planets with their icy moons.

The emerging protoplanets did not stay where they formed. Complex gravitational forces between the protoplanets, the disc of gas in which they were growing and the growing Sun caused planets to migrate in towards the Sun. We see some solar systems around other stars with giant gas planets so near to their star that they are red hot, others with planets with orbits so close together they cannot have formed there originally. Alternatively, planets can also be thrown out of their solar system and become so-called run-away planets. This speaks to a violent and chaotic early youth of many solar systems.

Ours was no exception. It is now generally accepted that very early in solar system history the primordial Earth collided with another young planet about the size of Mars in a collision that vapourised much of both bodies and threw a huge cloud of white-hot, boiling rock into orbit around the Earth. Most of the mass of the two settled back and cooled to form the planet we know today. The rest stayed in orbit, condensed, cooled and formed our Moon.

A natural satellite the size of our Moon is unusual, but may be important for the later developing biosphere on our planet, because it stabilized Earth's spin axis, keeping surface temperatures in a more narrow range. It also exerted tidal forces onto the young planet, which were much stronger than today, with repercussions on the heating of the interior of Earth, and also for coastal habitats once water condensed from the atmosphere to form oceans.

The Moon-forming impact was the largest impact Earth experienced, and it vapourised the crust. We can be confident that the Earth had no life immediately after the Moon-forming impact. After the impact the Earth's interior continued to separate into mantle and core, and some sort of crust formed again (we do not really know when, or how thick it was). The atmosphere stabilized in composition, with nitrogen and carbon dioxide gas as major constituents. Water appeared on the surface but again it is a measure of our limited understanding of those days that it is not clear even now whether that water primarily came from the primordial Proto-Earth or from comets hitting the Earth after the Moon-forming impact.

However, even after that event Earth continued to be hit by asteroids and comets, but in gradually declining numbers, perhaps with occasional surges, such as a period called the Late Heavy Bombardment (LHB) between 4.1 and 3.8 billion years ago. This is also the time period for which we find the first evidence of life on Earth based on geochemical (isotopic) and fossil evidence (Box 1.2). The origin of life might have occurred rather fast, perhaps even before the Late Heavy Bombardment, almost as soon as conditions on the surface became tolerable to life.

The biochemistry and structure of that earliest life is unknown. Certainly, it was unicellular, microscopic, and anaerobic (thriving without oxygen). This type of life still persists till today. As a general principle the overwhelming majority of life on Earth stayed small and simple. We don't think that the first organisms were able use light as an energy source, but photosynthesis did arise fairly early, probably about 3.5 billion years ago, if not earlier. As we will discuss in Chaps. 4 and 5, the ability to capture light and the ability to use that energy to make oxygen are two different things, but life had probably mastered both by 2.7 billion years ago. However, that early oxygen was consumed by reactions with surface minerals, volcanic gases and organic matter (for example, deriving from dead organisms), and so almost none built up in the atmosphere until about 2.4 billion years ago, when oxygen levels started to rise in what is called the Great Oxygenation Event (GEO). During or shortly after the GEO, Earth experienced widespread glaciation, a so-called Snowball Earth event about 2.3 billion years ago, likely as consequence of the rise of oxygen in the atmosphere and a drop in greenhouse gases such as methane and carbon dioxide. During this long-lasting Snowball Earth event all or most of Earth was covered by glaciers.

The rise of atmospheric oxygen, produced by cyanobacteria, apparently led to the first global crises of biology. Nearly all organisms at this time were anaerobic and oxygen was a toxic compound to them, as it is to many anaerobic microbes today. Only gradually did life learn to live with that reactive chemical, and to capture and use the large amounts of energy to be gained from reacting oxygen with organic matter. Eventually the ice retreated and the climate warmed up again, coinciding with the appearance of the first eukaryotic organisms in Earth's fossil record. Scientists still debate whether these events were linked, or whether the timing at the end of Snowball Earth is a coincidence. It could even be that the event occurred hundreds of millions year earlier or later given the scarce fossil record. The (slow) march toward complexity continued. Genetic evidence and first fossils are hinting that multicellular organisms appeared over 1 billion years ago, although fossils that are unambiguously from multicellular organisms have only be found in rocks 650 million years old or younger. With the rising oxygen levels, more and more complex multicellular organisms could be sustained, though they probably remained small and sluggish compared to animals today. About 650 millions years ago Earth experienced another Snowball Earth event, but life re-radiated with an explosive diversification of structural forms and life-styles after the Earth warmed up again, providing a whole set of newly available habitats once the ice retreated.

This time period is referred to as the Cambrian Explosion, about 541 million years ago, at the start of the Cambrian Period (Box 1.2). It is characterized by animals with hard shells, an innovation that protects against active predators, which implies that predators had evolved too. Shells and exoskeletons have evolved many times independently, showing the value of this adaptation. With the advent of macroscopic life forms with hard parts scientists gained a continuous sequence of a well-preserved fossil record from which we can deduce further evolutionary progress toward complex life.

The path of complex life has not been easy. A number of events, called mass extinction events, have wiped out many of the species on Earth. The largest mass extinction event was the Permian extinction event about 252 million years ago, in which about 95% of marine species and 70% of terrestrial species became extinct. This was also the only extinction event in which insects took a severe hit. It might have taken up to 10 million years for life to recover completely and repopulate all the environmental niches. The extinction event showed that the subsurface of the oceans and subterranean land habitats provide much more stable environments than near-surface habitats, which took the brunt of the extinction event. But life did rebound, underlining the biological principle that individual organisms and even species are fragile, but life as a whole is hardy. The newly available heterogeneous environments and new habitats promoted a large degree of biodiversity of large animals and plants.

The best known mass extinction event happened much later, when much larger and more anatomically and behaviourally sophisticated animals had evolved. This was the extinction event that wiped out the dinosaurs at the end of the Cretaceous, and laid the path for today's mammal-dominated large animal ecology. But this was not nearly as severe as the Permian extinction. We should note, however, that no mass extinction event has come close to wiping out life. The disasters are total for individual species, sometimes for whole classes of animals or plants. But animals, plants and fungi with the same *functional* abilities arose again after the Permian extinction to replace the old after 5–10 million years. When the Chicxulub asteroid wiped out the dinosaurs, it did not take long before large animals roamed the Earth again. The mammals survived, and were waiting in the wings to take centre stage.

Eventually, about 7 million years ago, our ancestor separated from the ancestors of chimps and gorillas, and around 2.8 million years ago a recognizable human species appeared.

Our very short run through the history of life on Earth shows that how life evolves depends on the planet. If there were less reduced rocks to react with oxygen, an oxygen-rich atmosphere might have arisen earlier. If the Chicxulub asteroid had not hit Earth 65.5 million years ago, the dinosaurs might still be around today. But equally life has modified the planet, changing its surface chemistry and its atmosphere. So when we ask whether another world might be habitable, we are not asking whether it is like Earth today. We are asking what basic parameters might prevent life ever arising, or surviving, on a different planet. With that in mind, we have to consider how the habitability of a planet relates to the astronomical conditions to which it is exposed.

2.2 Astronomical Constraints on Habitability

Whether a planet or moon is habitable depends on its position in space and time. Some unfavorable locations are straightforward, like being located near a black hole or in the immediate vicinity of a star that goes supernova. Some other parameters are more subtle. Solar systems that formed very early in the history of the Universe were composed only of hydrogen and helium, and so had no heavier elements (known to astronomers as ‘metals’, although that also includes things that in everyday language are not metallic at all, like oxygen or carbon). These solar systems would have had no dust, and would be unable to form rocky planets. The important heavier elements that life needs, such as iron, are created when a star goes supernova, and so would have been missing from these first systems.

Not all rocky planets forming after that initial wave of solar system formation are habitable. Geoscientist James Kasting has defined that region around a star where a planet could support life as the Habitable Zone (HZ), the zone in which a planet similar in mass to Earth would retain an atmosphere and liquid water on its surface. The presence of liquid water is thought to be an important precondition for most, maybe all forms of life. The HZ is quite narrow for most stars and the position and extent of the HZ depends primarily on the total amount of energy emitted by the star. However, even for the same type of star the exact boundaries of the HZ depend also on the planet’s geophysical and geochemical characteristics, particular its mass, albedo (the amount of light it reflects back into space), and the thickness and chemical composition of its atmosphere. All of these parameters affect the rate at which water escapes from the planet's atmosphere near the inner edge of the zone, and the chance of global refrigeration near the outer edge. Most models indicate that the inner edge of our Solar System's HZ lies between 0.95 Astronomical Units (AU—the average distance from the Earth to the Sun), where Earth's stratosphere would become moist and water would leak into space, drying the Earth out, and 0.84 AU, at which Earth's surface temperature would climb dramatically due to a run-away greenhouse effect, an effect that is observed today on Venus and renders that planet completely uninhabitable.

The outer edge of the HZ is determined by the formation of carbon dioxide clouds, which cool a planet's surface and mean that carbon dioxide, a key greenhouse gas in our atmosphere, would 'snow out' of the atmosphere as solid CO_2, like it does on the poles of Mars. The outer edge is located between 1.40 and 1.46 AU in our Solar System. However, the HZ could extend theoretically beyond 2.0 AU if Mars would have a larger mass or a thick atmosphere with a strong greenhouse effect. Mars is at an average distance of 1.52 AU.

Venus is located at 0.72 AU and not in the HZ today, but it used to be in the HZ early in Solar System history. Like all stars of its size, the Sun's output of energy has increased by about 30–40% since it formed 4.54 billion years ago, and so the boundaries of the HZ have moved outwards. Four billion years ago Venus was in the HZ, today it is not. In the distant future the HZ will continue to move outwards, and the Earth will then also suffer Venus' fate.

By analogy to the habitable zone (HZ) around a star, the term of a Galactic Habitable Zone (GHZ) has been advanced as well. The cores of many galaxies, including our own, are violent places, with densely packed stars and a supermassive black hole whose proximity would disrupt solar systems, and whose radiation output would make habitability unlikely. The GHZ is defined as that region in a galaxy where those heavy elements needed by life are available and where any life would be far enough away from the galactic center so it is not exposed to too much radiation or too high of a frequency of stars going supernova. The GHZ has been modeled by Charles Lineweaver, who quantified it as that region between 7 and 9 kpc (23,000–29,000 light years) from the galactic center that widens with time and is composed of stars between 4 and 8 billion years old. The underlying assumptions for a GHZ were based on (1) the presence of a suitable host star, (2) sufficient heavy elements so terrestrial planets can form, (3) enough time to allow for biological evolution, and (4) a region of space without life-extinguishing supernovae.

The concepts of the HZ and the GHZ are useful screening tools. But a planet in the HZ is not necessarily habitable. A rocky planet orbiting in the

HZ is “Earth similar”, but it need not be habitable. An example is our Moon, which is a rocky planetary body in our Solar System’s HZ, but is not habitable. Rather, we are looking for an Earth-like planet, a planet with the right combination of surface physical and chemical features to make it a suitable place for a sizeable biosphere including the presence of complex and macroscopic life. This may include orbiting in the HZ, but ironically may not. A world like Jupiter’s moon Europa has a stable deep water ocean, but may be under miles of ice. Europa orbits far outside the HZ and despite its orbit, Europa’s ocean may be habitable, and one of the hottest topics for future space exploration is to see if it is in fact inhabited. Even on the surface of a world, a life style that cycles between dormant and proliferative forms may be possible on a planet that is outside the HZ most of the time, as its life forms may require only periodic stability of liquid water on a planetary surface; a notion which might be relevant for Mars. Thirdly, life may utilize radically different biochemistries, even other solvents than water such as the liquid hydrocarbons on Titan, which exist stably on that moon’s surface. Such completely different life would require different HZ requirements around a star.

Most stars are much fainter than the Sun. Particularly common are the dim, small, red stars called M dwarf stars. More than 75% of stars in our corner of the Universe are M dwarf stars and stars like our Sun, a G dwarf star, are actually quite rare. The nearest star to the Sun (Proxima Centauri) is a red dwarf, although it is too faint to be visible to the naked eye. Many of these stars, including Proxima Centauri, have been shown to have planets around them, but scientific opinion has historically varied on the suitability of M dwarf stars for life. Planets around M dwarf stars have certain advantages as abodes for life, but also challenges. An overview of those is provided in Table 2.1. Initially it was thought that they could not be habitable, because the HZ of a planet orbiting them is much closer to the star, meaning that most of them are tidally locked. This means that they always show the same face to their star, like the Moon always shows the same face to the Earth. If you stood on the surface of such a world, the Sun would stay in the same place in the sky, never rising or setting. Thus one side of the planet would heat up tremendously, while the other would be extremely cold. However, modeling showed that an atmosphere, in principle, could balance these temperature peaks to an acceptable degree, so that might be less of a barrier than originally thought. But the greatest challenge is probably that M dwarf stars have huge solar flares, especially while still being young, which can be so violent to blow away the atmosphere of a whole planet, leaving it fundamentally uninhabitable.

Table 2.1 Properties of red M-dwarf (dM) stars and their relationship to planetary habitability

M-dwarf star property	Astrobiological assessment
Nearly constant luminosities over tens of billions of years	M-dwarf planets provide a stable environment for life to form and evolve within fixed habitable zones later in their life time
M-dwarf stars are ubiquitous, comprising more than 75% of stars	High chance for at least some habitable planets
Long life times (larger than 50 billion years)	Especially beneficial for evolution of complex/intelligent life, because of greater evolutionary time span (compared to the 7 billion years Earth is habitable, and the 4 billion years for evolution to complex life on Earth)
There are many old M-dwarf stars, older than 5 billion years, in our Galaxy	Very old, metal poor, M-dwarf stars would likely not be able to form rocky planets because of the paucity of metals. A low metal environment would also be problematic for the development of life
Theoretical studies indicate that "Super Earths" can easily form in the protoplanetary disks of M stars	Planets hosted by M-dwarf stars should be at least as common as those hosted by Sun-like stars. Even without much effort, several M-dwarf stars have been found to host planets
HZ is located very close to the host star at $<$0.1–0.4 Astronomical Units (AU)	The planet would easily become tidally locked, reducing likelihood of global habitability
HZ of a young M-dwarf is much further from the star than that of a mature star	Planets near to a M-dwarf may be "baked dry" when the star is young preventing them being habitable when the star settles down in its 'middle age'
Unlike Sun-like stars, M-dwarf stars have essentially no photospheric continua in the UV ($<$2500 Å), because of their low temperatures	While generally harmful to organisms, UV irradiation is a powerful force in evolutionary adaptation, and may also play a role in the origin of life
M-dwarf stars have very efficient magnetic dynamos resulting in strong coronal X-ray, and different types of UV emissions	While generally harmful, these types of radiation can be filtered out by planetary atmospheres and may be evolutionarily beneficial. However, strong flares can erode the atmosphere and make life impossible

However, once they have settled down to a stable, quiet middle age, M dwarf stars are very stable, and do not change their energy output, so their HZs do not move outward as the HZ of our own Sun does. This suggests that, if a planet around an M star can survive the star's unruly youth, then it would be more likely to remain habitable. So perhaps, the best type of star for habitability and life are main sequence K stars, which are in between M and G dwarf stars.

There are other astronomical parameters that favor or disfavor habitability. For example, most stars in the Universe seem to be binary stars. It is harder to evaluate these systems in regard to stable planetary orbits and variations of surface temperatures.

2.3 Planetary Requirements on Habitability and Life

Requirements for habitability and life on other planets have been extensively discussed in the scientific literature. The approach taken by the research group led by one of the authors of this book was to develop a so-called Planetary Habitability Index or PHI, which is based on essential requirements for all life and includes the presence of various planetary parameters such as a suitable substrate, the availability of energy, the abundance of complex carbon chemistry, and the presence of a liquid solvent.

A Suitable Substrate Is Needed for Life We have talked above about rocky planets, but not explained why we only consider these as suitable for life. Life thrives particularly at discrete interfaces, especially between solid and liquid substrates. Even on a larger scale we often observe lots of biomass and biodiversity at these boundary environments such as river banks, lake shorelines, and coastal ocean areas. Rocky planets like Earth provide interfaces between their solid features and any liquids or atmospheres that may be present. The surfaces of solid materials provide a physical restraint to movement, potential islands of habitability, where organic compounds in contact with liquids or an atmosphere can accumulate and microbial colonization can take place—rather than being swept away in a pure liquid or gaseous medium. The presence of a solid substrate such as rocks or ices promotes habitability by providing a higher density of chemical compounds, a larger degree of stability, and a surface for chemical reactions. A solid substrate can also protect life below that surface from various types of radiation such as UV light or the radiation from Jupiter's radiation belts in the case of potential life in the subsurface ocean of Jupiter's moon Europa (further discussed later).

Planetary Mass Related to the need for a surface is the need for a minimum mass. Asteroids and small moons cannot generate enough internal heat to power volcanism and the regeneration of their surfaces. Planetary cores with a high density generate internal heat from radioactive decay. The heat pushes out the volatiles in the crust and mantle of a terrestrial planet contributing to the build-up of an atmosphere. On Earth, internal heat powers plate tectonics, which provides one of the best recycling mechanisms for minerals and nutrients, which in turn is needed to support a sizable biosphere. If a planet exhibits plate tectonics it will inevitably lead to the topographical complexity and geochemical cycling as experienced on Earth, and possibly early Mars and early Venus. On Earth-like planets geochemical recycling of carbon by tectonic processes is generally considered critical for stabilizing the climate of the planet against variations in radiation output from the planet's central star. Larger rocky planets will also heat up their interior enough for that the iron melts and collects in a liquid metal core, as happened on the Earth. This core will generate a magnetic field, which may be an important requirement for a habitable surface. Our magnetic field protects the atmosphere, and the surface, from large surges of charged particles from our Sun called coronal mass ejections. It might be that only a strong geomagnetic field, at least the strength of Earth's field, would provide sufficient protection from coronal mass ejections, which might otherwise sterilize the surface and possibly strip away the atmosphere over time, a danger existing for all planets around stars that we think could support life (main sequence G, K , and M stars). Another danger is superflares, flares that are 100 times stronger than the strongest solar flares we see on our Sun today, which can occur when the stars are still young.

Diversity Is Good Because life thrives at interfaces, a diversity of environments encourages more life. But this does not seem to constrain our search much. Every terrestrial planet or moon we have examined in the Solar System shows a stunning diversity of environments even if they are unimaginably hostile to life. Mars has mountains on which the temperature never rises above −40 °C, and canyons where satellites may have detected flowing water. Jupiter's moon Io exhibits a landscape of lava flows, lava lakes, and giant calderas surrounded by sulfur dioxide frost. Volcanic geysers are spewing sulfurous plumes up to heights of 500 kilometer or more. Saturn's moon Titan resembles early Earth conditions in many ways with clouds, storms, sand-dunes and lakes, even though the sands are made of ice and the lakes of a liquid methane-ethane mixture. Even Pluto, long thought to be an inert ball of ice and rock, was revealed by the New Horizons probe in 2015 to be covered by a huge variety of terrains, some geologically quite recent. Diversity seems to be a universal on smaller, rocky bodies in our Solar System, and we have no reason to suppose it does not occur elsewhere.

The presence of an atmosphere promotes habitability because it protects the surface from UV irradiation and other detrimental shortwave radiation that is damaging to life. An atmosphere also distributes heat from one side of the planet to the others, thus counteracting harmful temperature peaks. It also stabilizes liquids on and near the surface of a planet which, as biological solvents, are essential for life. Two interlinked processes are at work. Firstly, the pressure of a substantial atmosphere stops the liquid from boiling away. This is why Earth has liquid oceans and the Moon does not. The Martian atmosphere today is too thin to allow liquid water to form on the planet's surface (except, perhaps, in some very deep basins or canyons), where ice warmed by the Sun goes directly into vapour without melting, a process called sublimation. Secondly, an atmosphere also protects the liquid from photolysis, the breakdown of a chemical by light. Other effects exist as well. For example, because of its structure Earth's atmosphere also provides a cold trap for water in the tropopause (the layer between the troposphere and the stratosphere), which keeps water vapour in the lower atmosphere, and prevents water from moving up into the higher atmosphere, where it would be broken down by photolysis and the hydrogen formed would escape to space, permanently reducing Earth's water supply. This may have happened as a later process on Venus.

The icy moons such as Europa, Ganymede, Enceladus, and Triton do not have a substantial atmosphere, but the protection and function that the atmosphere typically provides can be taken up by their icy crust, which protects the underlying liquids, potentially oceans, from photolysis and boiling away, thus possibly providing a suitable habitat for life. In this special case an atmosphere might be not be needed at all, at least not for microbial life to thrive.

The Availability of Energy Is Critical for Life Life needs energy in two ways. Firstly, the Sun is critical to making the Earth warm enough to be habitable in the first place. Without a central star like our Sun, the surface of every rocky planet in our Solar System would be so cold to make life on it impossible. Stellar energy is not the only source of planetary heat, although it dominates on Earth. Another is internal heating from radioactive decay or gravitational contraction. Jupiter gives out four times as much heat as it receives from the Sun due to internal heating. This however rarely heats up small planets much. A third source of heating is tidal flexing. The pull of other bodies stretches and compresses the Earth itself, as well as the more familiar rise and fall of the oceans. This flexing of the planet releases heat. Tidal flexing can generate lots of energy. The tidal flexing caused by Jupiter in its moon Europa keeps its subsurface ocean in liquid form, and drives sulfur volcanism on the moon Io; Io is the most volcanically active body in the Solar System.

However, life also needs energy more directly, to power its chemistry. The most important energy sources of this chemical energy for life on Earth are visible light and redox-chemistry. We will discuss how life evolved the capability to capture light energy in Chap. 4. Light is ubiquitously available in solar systems. The amount of light received by a planet depends on the type of the star (specifically its mass, and hence both its temperature and size) and on the planet's distance to its central star. The amount of light intercepted by a planet drops off in proportion to the square of the planet's distance from the star; for example a planet twice the Earth's distance from our Sun would only receive one quarter of the sunlight. Nevertheless, there is much light available, even in the outer Solar System. For example, enough light still reaches Saturn's moon Titan to make Earth-type photosynthesis possible, in principle, even though Titan is 9.5 times further out from the Sun than Earth.

Redox-chemistry, which can be based on inorganic compounds or organic compounds requires a dynamic planet, in which elements are constantly recycled between the different oxidation and reduction states. On Earth this happens either because life itself reprocesses the chemicals, or because geological processes powered by Earth's internal radioactivity do.

In principle, other energy sources such as thermal gradients or magnetic fields could also be used to power metabolism, but the energy yields are generally small compared to light and redox-chemistry. Nevertheless, under certain planetary conditions this option for life should be considered.

Organic Carbon Chemistry Provides Building Blocks for Life Carbon's ability to form complex, stable molecules with itself and other elements, particularly hydrogen, oxygen, nitrogen, phosphorus, and sulfur is unique. Carbon and its chemistry (called "organic chemistry") involves millions of compounds, including many polymeric compounds. Carbon is the universal building block for life as we know it. Other elements can form complex molecules, notably silicon, which can form complex compounds, including polymers. However, these tend to be too stable (like rocks—unable to engage in the dynamic chemistry of life) or too unstable. Carbon would be expected to outcompete silicon as a building block in nearly every imaginable planetary scenario. The presence of organic carbon compounds, especially complex organic compounds and polymeric carbon compounds would be a strong indicator for habitable conditions and perhaps even life itself. It is not 100% clear that life needs to be based on carbon chemistry, although that seems a reasonable assumption. Of course, that carbon chemistry need not be the DNA and proteins we find in terrestrial life. We know of one, extraordinarily powerful, flexible form of life that uses proteins and DNA dissolved in water, and thus many scientists assume that those are requirements for life. But the evidence for this is pretty thin.

The Presence of Liquids Is Essential for Life's Need for a Suitable Solvent The presence of liquids in the atmosphere, on the surface, or beneath the surface is a function of chemistry, pressure, and temperature of the planet or moon. A solvent is needed so that molecules can move and react. Life is dynamic chemistry, so molecules have to be able to move, and the solvent enables this. A biological solvent must be able to dissolve many chemicals (which are then called solutes), while enabling some macromolecules to resist dissolution and so provide boundaries, surfaces and interfaces such as the walls of cells or the bones of animals. This need for a solvent provides both an upper and lower limit to the temperatures and pressures at which biochemistry can happen. A solvent also provides a buffer against environmental fluctuations.

In order for a solvent to be suitable for life, its physical properties in the liquid state must be matched to those of the environment in which it occurs. We do not think that this suitable solvent needs to be necessarily water. Although most life would be expected to be based on water in some way, other liquids could take over the functions as a solvent such as methanol or ammonia. The emphasis is again on function, not on a particular structure or chemistry. As we will later see this principle also applies when we discuss biological diversity.

Our roundup of what makes a habitable world has been quite broad. We have tried to stay away from describing a habitable planet as "Earth-like", what we might describe as the Earth-centric trap. We only know of one occurrence of life in the Universe, and that is life on Earth. Thus the challenge is to decipher which characteristics of life on Earth is a universal attribute of life and which is specific to life as we know it.

We are not convinced that the above discussion provides an exhaustive list of requirements for life nor that these are absolute requirements for primitive life. A case in point is the suggested requirement of an atmosphere, the function of which can be replaced in the case of a subsurface ocean habitat with an ice cover. Requirements become a bit more clear (and stringent) when discussing the habitability requirements for complex, macroscopic life.

2.4 Habitability Requirements for Complex, Macroscopic Life

Though the requirements for habitability as reflected upon above are necessary, they are not sufficient for identifying the planets most likely to be amenable to the evolution of a higher degree of biological complexity.

What do we mean with complex life? The simplest microbe is a highly complex structural, chemical, and informational system, as complex as the most sophisticated machines that humans have made. However, they have a limited repertoire of behavior (physical and chemical). When we talk about complex organisms, we refer to an increasing diversity of internal structure, organized on an increasing number of levels. A nerve cell in a fruit fly is more complex than a bacterial cell in the number of genes within it, and the number and structure of internal compartments that make it up. It can also show a greater range of behaviours (although its tolerance for greater extremes of environment is far less). But more than this, it also contributes to a nerve tissue, which is itself complex, and that nerve tissue contributes to a whole organism, which is therefore *much* more complex than a single bacterium. It is generally true that ecosystems reflect that complexity. Life forms are part of a larger ecosystem consisting of a variety of organisms in multiple trophic levels that occupy a variety of ecological niches and a range of life histories, and the more diverse and complex the life histories of the components of that ecosystem, the more complex the ecosystem as a whole. Thus the characteristics of the planet must be capable of supporting the complex ecosystems that complex life generates and needs.

These include the following:

Space to Grow Complex life tends to be bigger than simple life. This is not only true of large, multicellular organisms like trees and elephants. Even the smallest multicellular organism is larger than a single cell (by definition), and the complex single cells that make up animals and plants are themselves larger than bacteria. While bacterial life can live in the crevices in rocks, more complex life requires more space.

But complex life requires an extensive biosphere for another reason. Complex life is a response to complex environments, which can come from two sources. The first is a vast, complex planet, much of which is habitable. If there are only a few, isolated, restricted habitats, then ecological theory says that life in them will also be simple. But most complexity in an environment comes from other life, in an evolutionary competition that evolutionary biologist

Leigh van Valen called The Red Queen's Race, after the Red Queen in "Alice through the Looking Glass", who said that to stay still in her topsy-turvy world you had to run as fast as you can, you had to run even faster to get anywhere. If the biosphere is small, then competition from other organisms is simple, and evolution rapidly converges on simple solutions. ("Rapidly" might take hundreds of thousands of years, but on a planetary time scale this is fast.) If the biosphere is large and diverse, then organisms are constantly competing with many others, which themselves are evolving more and more sophisticated survival strategies. Becoming ever more complex is one way of staying ahead in this evolutionary arms race—not the only way, or even the most common, but one that is an option in a large complex biosphere. So for the evolution of complex life we do not just want a world that has a few small habitable spots, as may be true of Mars today. We want one that is habitable over a substantial fraction of its surface.

Time Is of the Essence The world also has to be habitable for long periods of time. The minimum time it takes to develop any particular level of biological complexity from a previous, simpler life-form is unknown, but we can guess it is much longer than the time needed to evolve simple life. Based not only on the history of life on Earth, but also on the presumption that natural selection requires a large amount of time to generate and test some of the solutions to the evolutionary problems that life faces, the planetary body which is host to complex, macroscopic life would have to be habitable for a geologically long time period. And it has to be continuously habitable by complex life. If the impact that wiped out the dinosaurs had been 1000-times bigger, and had wiped out all but a few hardy species of bacteria, it might have taken over 500 million years to re-build a complex ecosystem complete with large, land-based animals, not the few millions that were actually required. While the extent to which time is required for any given stage of evolution to be reached is uncertain, the empirical observation from life on Earth is that major transitions or key innovations, such as the appearance of multicellularity and the emergence of oxidative respiration, occurred over billion-year time scales. Thus, assuming a similar rate of evolution as on Earth, we would not expect to find complex life on planets around O, B, A, and F main sequence stars. These stars burn faster and hotter than our Sun, and planets around them would not have enough time to evolve complex life before the star expands into a red giant and swallows any habitable planet. Even our Sun, which increased in luminosity already by 30–40% since the early Solar System days, will render the Earth uninhabitable one day, first to humans in about 1 billion years, and then to all life in about 2.5 billion years as the increasingly bright Sun turns the last habitat on Earth into an uninhabitably hot, scorching desert.

Temperature Ranges Are More Constrained for Complex, Macroscopic Life than for Microbial Life It is observed that, while microorganism can grow at temperatures between −20 and +120 °C, all multicellular organisms can only grow at −10 to +70 °C. Animals and plants are limited to a range of −5 to about 60 °C. Some animals can survive temperatures far lower than this, because their large mass and good insulation buffers them against the cold. No animal can reproduce at higher temperatures (a few can survive temperatures as high as 150 °C by becoming dried-up, dormant 'tuns' or 'cysts' as tardigrades can, but they need to return to lower temperatures to move, eat and reproduce). There is no reason to suppose that complex life evolving on hotter worlds should not thrive at higher temperatures, but the range of temperatures at which they can grow and reproduce is likely to be more limited than the range tolerated by microorganisms on those planetary bodies. Thus, complex and macroscopic life is more likely to evolve on planets and moons that maintain temperatures within a particular optimal range. However, we do not know what that optimum is, apart from the case of life on Earth.

2.5 How Often Are the Preconditions for Complex, Macroscopic Life Met in the Universe?

The components for life are common. Organic molecules have been found in star forming regions, around protoplanetary disks, in meteorites, in comets, and in deep space. Water is among the most common molecules in the Universe, and a host of other liquids that might serve as solvent can exist at planetary temperatures. An abundance of light and heat and many other forms of energy are locally available and probably on many other planetary bodies. Rocky planets are likely to be common. As our methodology improves to detect exoplanets we are not only discovering large gas giants but also more and more Earth-size planets, some of which orbit in the habitable zone of their parent star, the zone where liquid water can exist stably on the planetary surface (Fig. 2.1). Soon we expect to also be able to detect Mars-size planets and exomoons, which are expected to be even much more common.

So the basic prerequisites for life are common throughout the Universe. However, we do not know how many of those planets are truly Earth-like

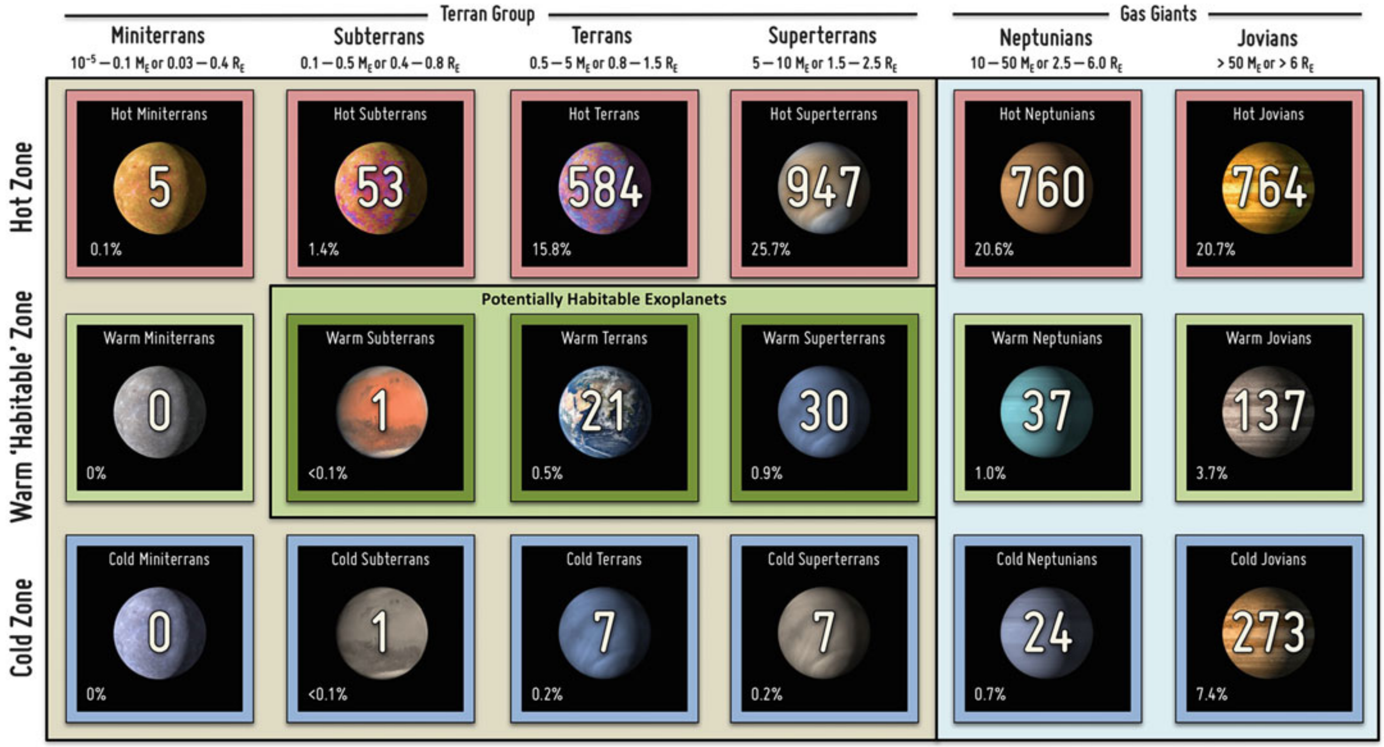

Fig. 2.1 Breakdown of Earth-size planets versus gas giants and projected temperature ranges. Figure is based on more than 3600 confirmed exoplanets as of May 2017, with credit to the Planetary Habitability Laboratory of the University of Puerto Rico at Arecibo. We doubt that Superterran worlds should be included in the assignment of potentially habitable exoplanets as we think that most of them are likely small Neptune-type gas giants, but this will be tested as our imaging techniques improve. With that improvement also more of the smaller planets will be detected, which will likely increase the number of possible habitable worlds

planets, i.e. with atmospheres, magnetic fields, active geology, surface water and the other features we have summarised above. Peter Ward and Ron Brownlee argued in their book "*Rare Earth*" that the Earth was subjected in its history to a set of more or less coincidental factors that are collectively highly unlikely. According to Ward and Brownlee, Earth is a statistical fluke, Earth-like planets are a rare occurrence, and so life also is a rare phenomenon. This must therefore be even more true of complex, macroscopic life, for which a larger set of these factors has to be met and habitable conditions have to endure for a much longer time.

However, Ward and Brownlee are asking how many other Earths there are. They may be right, there may be very few, just as there was only one Mozart and one Beethoven. But that does not mean that there have only ever been a handful of composers in history—other styles of music from Bach to "boy bands" are also music. In this book we are concerned with the music of life, not just the one composition played on Earth, with the basic functions of life, which evolved one way on Earth but could evolve elsewhere under other circumstances. Thus, a very different type of life could have evolved in the subsurface oceans of Europa or in the hydrocarbon lakes of Titan. None of these environments are the least Earth-like, but nevertheless could support something showing all the *functional* features of life, even perhaps complex life.

Indeed, René Heller and John Armstrong went recently to the extreme suggesting that some planets that are unlike Earth in other solar systems may be better suited for life than Earth. According to them, such "superhabitable" worlds would likely be larger, warmer, and older, orbiting K dwarf stars. Intriguingly, Earth might have been more habitable than it is today, because of a higher rate of tidal flexing during early Solar System history (our Moon was much closer). The importance of planetary history in determining whether a planet or moon contains life can also be seen on the example of Mars. Mars was a habitable planet a few hundred million years after its formation, when it had liquid water bodies on its surface. Today it appears to be too cold and dry for life, with no liquid water stably existing on its surface. At best we would consider Mars today being borderline habitable.

Of course, saying that a planet is habitable and saying that it is inhabited are two very different things. This chapter has been about whether a planet could, in theory, sustain life. That makes no predictions at all about whether there is life there, or what that life is like. This is a common misconception made during many of the announcements about a new discovery of an Earth-size exoplanet, insinuating that Earth 2.0 has been discovered. As it is clear from the previous discussion, there is much more to an Earth-like planet or Earth 2.0 than a similar mass and being located in the habitable zone. Earth-like planets may be rare indeed. And no planetary discovery yet has given any hint whether there is life on that planet. Even in the case of Mars, which has hosted 12 landers, numerous orbital missions, and been studied intensively from Earth through telescopes for over 200 years, we are still not sure if it is inhabited or not.

We conclude that the preconditions for life are common, but not universal. Not all stars are suitable, only a few planets around those stars are suitable even in principle, and they have to fit a rather strict set of criteria, albeit not that they be 'Earth-like'. But there are 400 billion stars in our Galaxy, and if only one quarter of one percent of those stars have a habitable planet that is still one billion habitable planets. Can even a handful of them harbor complex life? In Part II of this book we walk through the evolution of complex life on Earth, and argue that most of the steps toward complex life can be shown from what we know of life on Earth to be highly likely to occur. In the next chapter we start with the first step on that path and ask how likely it is that life arises on a habitable planet? How many of the habitable planets are really inhabited?

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Part II

Major Transitions in Earth's Life History

3

The First Cell and the Origin of Life Challenge

3.1 Early Attempts to Understand the Origin of Life on Earth

The most monumental event in life's history on our planet is its origin. Many early scientists, trying to understand the phenomenon of life, thought that 'dead' matter and energy alone cannot explain life, and that there must be a vital essence in living organisms that distinguishes them from the non-living world. Our current understanding refutes this, and shows that life is a chemical system, and follows the same rules as any other chemistry. The chemistry of life is extraordinarily complicated and intricate, but it is still chemistry. That living chemistry must have arisen from the non-living chemistry of its environment. However, despite nearly 150 years of modern science since Darwin speculated on life's appearance in 'some warm little pond' in his letter to J. D. Hooker on 1 February 1871, we still do not know how life originated on Earth.

3.2 When Did the Origin of Life on Earth Occur?

Starting with the basics, when did life appear on Earth? Life was definitely present on Earth 3.8 billion years ago, and may have been widespread as early as 3.5 billion years ago. More recent research indicates that life might have been around as early as 4.1 billion years ago (although this conclusion is controversial). Approaching the time window from the other side, from the

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formation of the Solar System, we now believe that about 4.5 billion years ago the planet that was to become the Earth was hit by another planet about the size of Mars in the impact that formed the Moon. This gigantic collision must have completely melted the crust of both planets. No living thing could possibly have survived this cataclysm. How long it took for the magma oceans to solidify and the vaporized water to condense into oceans in order for Earth to become a habitable planet is unclear, but it must have been many millions of years. So we know that life could not have appeared on Earth earlier than about 4.5 billion years ago.

If life appeared between 4.5 and 3.8 billion years ago, this leaves a window of maximum 700 million years for life to have arisen. In this time window the critical steps toward the establishment of life on our planet must have occurred.

This is relatively fast in geological terms. Many scientists argue therefore that the origin of life was not a highly improbable event. However, this argument does not necessarily hold. Granted, this amount of time is a relatively short time span compared to the total age of planet Earth, smaller than 15%, and perhaps smaller than 5%. However, even if the chances were astronomically low that life should arise in that time, the mere fact that we are here means that life had to arise in that time. Maybe it did so on only this planet, out of billions of billions in the Universe. Are we therefore incredibly lucky to be here at all? But if it had *not* happened, then we would not be able to contemplate this question, so it had to happen somewhere for us to be writing this book. (This rather annoying argument is called the Weak Anthropic Principle—we have to be here to discuss why we are here.)

So we are left with the unsatisfactory conclusion that the timing of the origin of life on Earth can only tell us that it is possible for life to appear on an Earth-like planet, but can tell us nothing about how likely it is that life appears on another planet. The origin of life may be so likely that it occurs on practically every habitable planet, or the origin of life may be such a truly exceptional event that it occurred only once in a galaxy or perhaps only once in the whole Universe, or it may occur in any frequency range in between.

3.3 How Life Arose

The timing of life cannot tell us how likely life is on a terrestrial planet like Earth. Equally, we would like to be able to point to many origins of life, and so argue for one of the models outlined in the introduction, but we cannot do that. So we have to delve deeper into how life might have arisen on our world. Unfortunately, that does not help much either.

The scientific community thought we would be close to knowing after the Miller–Urey experiment in 1952. In this famous experiment Stanley Miller and Harold Urey attempted to simulate the chemistry of the early Earth, when life is thought to have originated, by exposing gases such as hydrogen, methane and ammonia to electrical discharges mimicking lightning (Fig. 3.1). They harvested a rich treasure trove of organic compounds, including amino acids, which are the most basic building blocks of proteins. However, disillusionment set in quickly when it was realized that amino acids are a far cry away from the complex organic macromolecules that any type of organism utilizes. In addition, later investigations revealed that the early Earth atmosphere had a

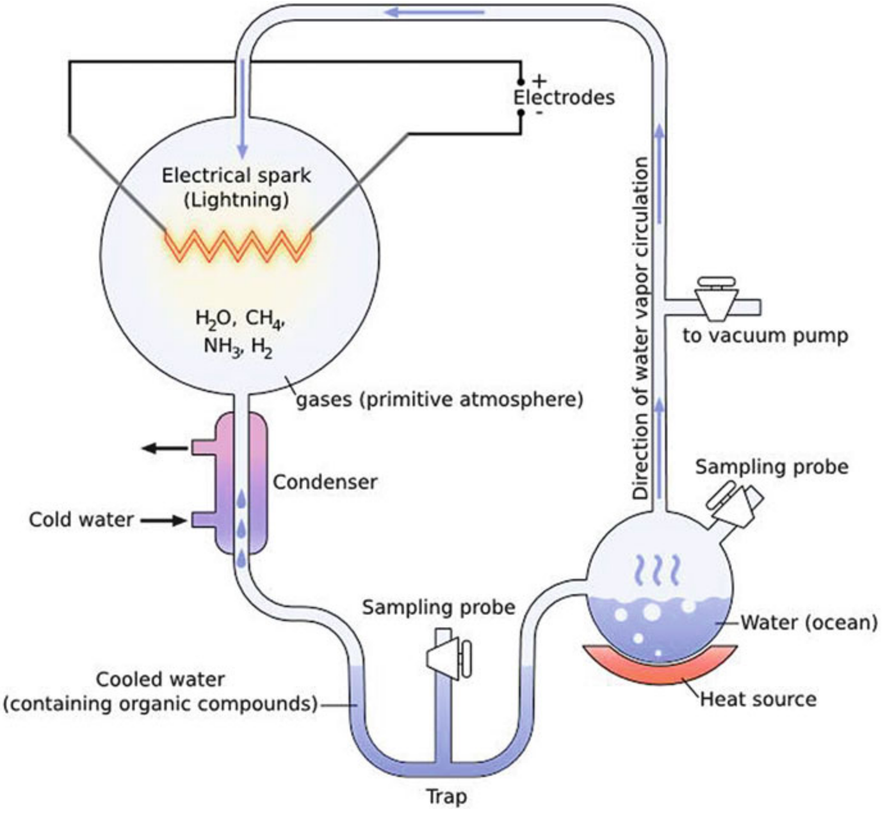

Fig. 3.1 Miller–Urey experimental set-up to simulate the early Earth environment (Creative Commons Attribution 2.5 Generic License)

different composition from that simulated in the original Miller–Urey experiment, in a subtle but critical way.

Chemicals can be described as ‘oxidizing’ or ‘reducing’, depending on how they react with each other (Box 3.1). Our modern atmosphere contains 21% oxygen, which as its name implies is highly oxidizing. It used to be thought that the early Earth had an atmosphere made of the reducing gases hydrogen, methane, and ammonia. However, more recently we realized that carbon dioxide was much more common in the atmosphere of early Earth, with much less reducing gases present. Repeating the Miller–Urey experiment with these more oxidised gases results in a much lower yield of amino acids. So the situation is more complex than life arising just from lightning in the atmosphere.

Box 3.1 Oxidation and Reduction

The terms ‘oxidizing’ and ‘reducing’ have deep roots in the history of chemistry. ‘Oxidation’ is the process of turning a metal into its powdery oxide, such as iron into rust. At the atomic level, what is happening is that electrons are being removed from iron atoms and given to oxygen atoms. ‘Reduction’ is turning the rust back into metal—‘reducing’ it, by taking electrons from another atom and giving them to the iron atoms. Hydrogen, the gas used to inflate the zeppelin Hindenburg, is a highly reducing gas, and can be used to give electrons to iron oxide in this way. Hydrogen reacts with oxygen releasing an enormous amount of energy, as the Hindenburg disaster showed. Other chemicals are generally intermediate between hydrogen and oxygen. Methane is a quite reduced gas made of carbon and hydrogen atoms, carbon dioxide is a quite oxidized gas made from carbon and oxygen atoms. Where all this oxygen in our atmosphere is coming from is discussed in Chap. 5.

3.4 The Puzzling Path to the Origin of Life

The first organisms on Earth were surely not as complex as the simplest organisms on Earth today. But that early life would still have to have the ability to self-replicate, a way to catalyze chemical reactions and obtain energy, and this would have to be in some sort of container to stop the chemicals leaching away. Modern biochemistry uses nucleic acids (DNA and RNA) as information stores, and mostly uses proteins as catalysts. As a simpler system compared to today’s microbes, the “Ribonucleic Acid (RNA) world” has been suggested in which RNA is both used as information storage and to catalyze chemical reactions. Peter Nielsen suggested an even more basic system called the “Peptide Nucleic Acid (PNA) world”, in which a blend of proteins and RNA called Peptide Nucleic Acids (PNAs) are used. Nielsen claims that under certain environmental conditions PNAs form more easily and are more stable than self-replicating RNA. Yet, all these ideas require a chemistry many orders of magnitude more complex than what we see in any natural non-biological environment. Evolution can generate astonishing complexity from simple beginnings. But until that basic combination of self-replication, metabolism and container is made there is nothing to evolve. So we are left with a fundamental, and as yet unsolved, problem.

Life is a molecular machine, and like all machines it needs parts and it needs a power supply. In chemical terms, the parts are the molecules of life—proteins, DNA, lipids and others—and the power supply is the chemical energy that life harvests from the environment. Without both you cannot have life, so which came first? There are at least four schools of thought—chemicals came first, energy was the initial step, both gradually evolved together, and neither came first—life was started on something else entirely.

The chemistry-first school points to the many ways that organic molecules that are similar or identical to the components of life can be made from inorganic starting materials like hydrogen, methane, and formamide. These could have been abundant on early Earth, and could have been made by volcanic or photochemical means ("photochemistry" is just chemistry that is powered by light). The simple building blocks for these compounds may have been delivered to Earth by comets, or they may have been belched out of volcanoes ("outgassed" in the jargon). From these simple materials the building blocks of proteins and RNA can be built, and from those building blocks the molecules themselves. The chemistry-first school of thought says that some combination of synthesis of complex chemicals was the key to assembling the first object capable of replicating itself.

Critics say that there is a vast gulf between such soups of simple molecules and the complex, dynamic architecture of biochemistry. It is like watching a toddler, hitting typewriter keys at random, typing the word "It", and saying "There, she has typed the first word of Charles Dicken's "Tale of Two Cities", obviously typing the rest is just a matter of time."

A particular issue with the 'chemical first' approach is that many of the key chemicals of life are actually not particularly stable if dissolved in water. Just accumulating chemicals is not enough. We need to have something more dynamic.

The energy-first school addresses this, saying that no chemistry, simple or complex, happens between stable molecules. What is needed is a source of energy to drive that chemistry. All sorts of systems that have energy flowing thought them tend to organize themselves into complicated structures and patterns. Examples abound on all scales, from the spiral patterns in water draining out of a bath to the complex structures of sunspots that are larger than the Earth. There are a range of ways that environments like tidal pools or volcanic vents generate chemical energy, and that can easily be coupled to making very complicated chemicals, and also potentially to organizing them into structures that could be the starting point for life. Furthermore, the best of these model systems generate energy in a way similar to the chemistry used by life, and there are plausible paths from this to using that energy to build really big, complicated molecules.

Critics say that this just produces chemicals, not an organized structure of chemicals that could itself capture and exploit energy. Returning to our toddler, if he or she accidentally sets fire to the carpet that would be poor evidence that the toddler had mastered the power of fire well enough to build a steam engine. And chemical reactions that are driven by energy generally just produce a complex mixture of chemicals that looks like tar (in fact, that is what tar is—a complex and entirely random mix of chemicals made by heating biological material).

The energy-and-molecules-first school recognizes the flaws in both arguments, and says that both must have evolved together. This is very sensible, but unfortunately it is rather hard to suggest a mechanism. A very specific combination of simple molecules and suitable energy needs to come together, then some very specific chemistry has to happen, most of which is not even tested in the clean and reliable conditions of a laboratory let alone in the outside world.

The last school says that the problems with all the above are insurmountable, and something else had to have happened. A common theme for this type of argument is that minerals played a major role in the origin of life, organizing molecules into structures that later became independent of the minerals that catalysed their formation. Did life start out on clay, only to leave its mineral origins behind later?

We do not propose to choose which of these is right. Rather, in this chapter we summarise this to show how far science is from agreement on even the basics. The underlying problem is that it is difficult energetically to build large organic macromolecules and then keep them from falling apart. This is why many origin of life researchers use organic solvents such as hexane to produce the organic building blocks of life in the laboratory. Even if organic molecules are the result of the experiments, the yield of selective and usable building blocks is rather low. Most of the yield is brown tar, a dead end for chemical reactions toward life. As an example, the amino acids from the Miller Urey experiment will only be stable for a short time period before turning into other molecules that are not useful for life. The majority of the material formed in the Miller–Urey flasks was a black tar-like material, in which the famous amino acids were a tiny minority of the chemistry occurring.[1] The required specificity may be the hardest problem of all for the origin of life. Turning a pig into sausage is rather easy, while turning a sausage into a pig needs a pig, it doesn't work without the genetic machinery and a very specialized chemical complexity that only exists today on Earth in living organisms.

Once a system that could couple energy dissipation to the synthesis of complex chemicals appeared, a number of further steps had to take place before anything that we would recognise as life emerged. These include synthesis and assembly of surfactant molecules into a boundary to contain the cell, development of molecules that could store information, appearance of a molecular assembly that could translate the information stored in that molecule, and selection and optimization of catalysts to make all this happen. It is very likely that some or all of these processes were helped by ions and mineral compounds in the early ocean. Many metabolic processes today use enzyme catalysts that contain clusters of atoms in arrangements very similar to those in minerals. Many of the experts in the field think that once RNA appeared it was, for a while, the major molecule of life, performing the role of catalyst and informational molecule in the time of the "RNA world". This could be the critical threshold from which we would call this self-replicating and metabolizing system "life".

However, there are large gaps of knowledge between nearly all of the steps outlined above. For example, how could largely chaotic or random interactions among simple organic molecules transition into reliably channeled and functioning metabolic pathways? How was the first RNA molecule formed? The link between the simplest early genetic codes and the sophisticated steps of protein translation we observe in an organism today appears completely elusive. The ribosome—the tiny protein machine that makes proteins in every form of life on Earth—contains more than 100,000 atoms in bacteria (the ones in eukaryotes—organisms like plants and animals—are even bigger). How did such an elaborate structure appear? There are also heated debates about the sequence itself—whether, for example, building a container (a cell) and a primitive metabolism preceded or followed development of the capacity for replication. All three events may even have occurred at the same time, because one without the other would have never resulted in anything resembling an organism. Energy (metabolism), information (genetic code) and semipermeable boundary (membrane) are all critical components and any type of structure without one of these critical components would have disassembled very quickly, or in the case of a lack of replication mechanism would have dissipated eventually with no chance of re-emergence. But how could that have possibly happened?

We do not want to imply that scientists have given up on the search for the origin of life. Many of the individual steps above have been probed in the laboratory, theories abound and are tested by reference to hard fact, not mythology. We will have a good idea one day. But that day might still be a long way off.

3.5 In What Environment Did Life Originate?

If we cannot tell how life originated, can we tell where it originated? That at least would give a clue as to whether such an environment was common, so we could at least make some guesses about what other bodies might independently host life. For example, if we know that life originated at hydrothermal submarine vents, then icy moons such as Europa would be good candidates for somewhere where life could originate, while dry desert planets would be not. Alternatively, if drying and wetting cycles that occur in transient desert lakes were critical for the origin of life, ocean planets would be excluded and any planetary bodies that contain an intermix of land areas and large water bodies would be favoured. If tidal land areas are needed for the origin of life, the only planetary bodies on which life could have evolved in our Solar System would have been Earth and possibly Saturn's moon Titan. Or, life might be able to originate under a number of very different environmental scenarios, which means that all these worlds could be possible abodes for life.

However, all of these kinds of assessments are tricky, because planetary histories span a large amount of time and environmental conditions can change drastically during these giant time spans. The best examples are our neighbouring planets Mars and Venus. Mars certainly used to have large areas of water on its surface, Venus probably did. However, nowadays Venus is an extreme greenhouse planet with surface temperatures hot enough to melt lead, and Mars a desiccated ice house.

A recent study in 2016 by William Martin from the Heinrich Heine University in Düsseldorf, who analysed more than six million protein encoding genes, supports the idea that life originated at a hydrothermal vent on the ocean floor (or more exactly, that the common ancestor of all modern life on Earth lived in such an environment). Many scientists favour the suggestion that life originated at submarine hydrothermal vents (Fig. 3.2). Ever since these vents were discovered in the 1980s, they have intrigued the scientific community. Minerals and gases stream out of these submarine

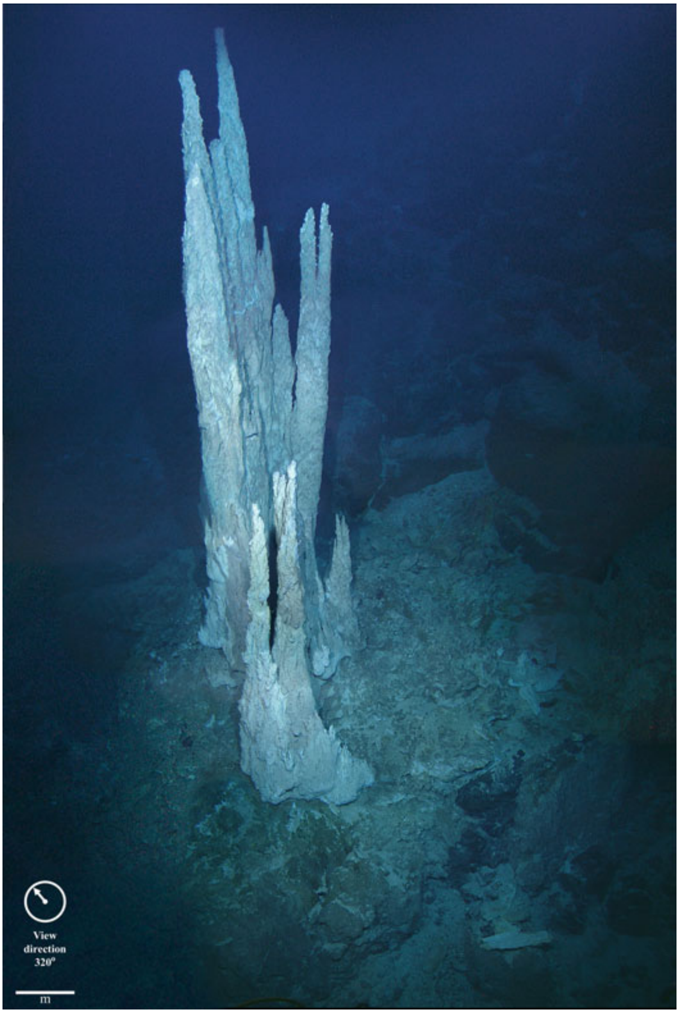

Fig. 3.2 Photomosaic of a 13 meter tall carbonate chimney called Ryan, a type of hydrothermal vent. Long term seepage of fluids from the steep cliffs bounding the eastern side of the Lost City Field has resulted in beautiful arrays of narrow pinnacles that reach many tens of meters in height. Credit: D. S. Kelley and M. Elend, University of Washington and URI, and NOAA Ocean Exploration

fissures, including hydrogen, methane, carbon monoxide and hydrogen sulphide. These are reduced gases (recall from a bit earlier that reduced gases tend to react with oxidized ones, and so it is at hydrothermal vents). Under the right conditions, the volcanic gases can react with atmospheric gases dissolved in the seawater to make chemicals like those in biochemistry.

These vents are hot, and intriguingly modern molecular studies suggest that the Last Common Ancestor (LCA) of all life on Earth was a thermophile—an organism that likes high temperatures.

However, that does not mean necessarily that life originated at those vents. After the Earth became mostly habitable the planet continued to be bombarded by asteroids and comets. The bombardment did probably not tail off until 3.8 billion years ago. The largest of these impacts could have rendered much of the surface uninhabitable. Life may have arisen on or near Earth's surface before 3.8 billion years ago, but had to retreat during the meteorite impacts to the dark depths of the oceans, only to spread again to the surface once the meteor bombardment subsided. The implication is that the Last Common Ancestor (LCA) of life on Earth, which is proposed to be a hyperthermophilic microbe living at the hydrothermal vents, was merely the Last Common Survivor from the period of the heavy meteorite bombardment.

But there are also geochemical reasons which would support an origin of life at hydrothermal vents, particularly because the next step toward increasing chemical complexity from amino acids upwards can occur here readily. Pioneering work by Günter Wächtershäuser has shown that amino acids can be activated by carbon monoxide and an iron-nickel surface at high temperatures to form peptide bonds. Peptide bonds are a critical step toward life, because they connect amino acids to form proteins and are challenging to form in water. This is because during the chemical reaction, called condensation, a water molecule has to be expelled while being in water, which is energetically unfavourable.

The idea of a hydrothermal origin of life leads to what is called an 'Iron-Sulfur' world view of the origin of life, where the chemistry of iron and sulfur are central to driving the formation of organic molecules, and coupling this to energy. Some of the Iron-Sulfur world's problems were addressed by William Martin and Michael Russell. They suggested that the first cellular life forms may have evolved at alkaline hydrothermal vents (a particular type of vent that is not as hot or, as the name suggests, as acidic as average vents). Their hypothesis is that life originated inside microscopic caverns that are coated with metal sulfides within these vents. These types of vents are typically located in the deep sea where continental plates are moving apart and new sea-floor is being built from mantle rock underneath—sites called Spreading Zones. The flow of water through the vents and their steep thermal gradients provides a continuous supply of organic building blocks and energy, while the micro-caverns provide the means of concentrating the newly synthesized molecules, thereby increasing the chance of forming organic macromolecules. This proposed path toward life also involves the incorporation of inorganic metals like nickel and iron, in conjunction with sulfur, which is mirrored in many critical life processes today. Furthermore, as later pointed out by Michael Russell, the iron sulfide mineral mackinawite could have played an instrumental role as it could have formed the first semipermeable membranes of life. Semipermeable membranes are (as the name implies) ones that are permeable to some molecules but not to others. A semipermeable membrane is critical for the first cell, because certain molecules such as nutrients have to be let into the cell and others, such as waste products, have to be discarded from the cell, but the cell's key metabolites, enzymes and genes have to stay inside and not leak out. In the Iron-Sulfur world the mineral itself forms a semipermeable membrane surrounding the micro-caverns, the cell only having to find a way to make its own when it became a "free-living" life form, independently from the vent system.

However, other ideas abound and include localities such as tidal flats or a cold water origin for life within brine-rich channels in water ice. There are even some suggestions that life might have originated in deep fracture zones within the Earth.

Tidal flats and temporary ponds provide a solution to a major problem for the traditional scenario of an origin in a "warm little pond". As mentioned above, many of the key molecules of life—DNA, RNA and proteins—are made by condensing smaller units together, releasing water. If you dissolve these polymers in water, they have a tendency to break up again, hydrolyzing back to monomers. Making protein from amino acids requires you dry the amino acids out. There are many ingenious schemes for how that can happen, but the end result has to be proteins and RNA dissolved in water, where they tend to fall apart again. Modern life overcomes this by constantly repairing and replacing its constituents. But before life started it could not do this. So we are left with the conundrum that early life had to be made from chemicals that are not that stable in water, and the only way to keep them intact was to have a living system made from those chemicals.

There are ways out of this dilemma though. In shallow water reservoirs such as tidal pools large amounts of shoreline would be exposed to continuous drying and wetting cycles which are driven by the tidal to and fro caused by the Sun and the Moon. In these pools a sequestration of organic molecules would occur, many of which would get continuously assembled and disassembled, with the result of a wide variety of polymeric compounds including peptides. Some support is also given to that kind of scenario based on the fact that our Moon was much closer to Earth about 4 billion years ago, around 25,000 kilometers compared to the current 400,000 kilometers (and it still retreats by about 4 centimeters every year), meaning that tides would have been drastically higher in the early days of our world, and as a result tidal landforms like beaches, tidal mudflats would have been larger and more common, and those rock-pools where today we search for crabs and anemones on the seashore would have been much more common. Tidal flats are typically rich in clays, which led to another proposition. Graham Cairns-Smith suggested that certain clay minerals might have served as an intermediate step between "dead" matter and organic life, meaning that the first life on Earth might have been based on clay minerals.

The sequestration and enrichment of organic molecules would not have to necessarily occur in a tidal flat. Other options exist. For example, Leslie Orgel showed that two of the building blocks of RNA and DNA, adenine and guanine, can form readily in ice due to freezing and thawing cycles, which also concentrate molecules dissolved in the water from which the ice forms. As the water freezes, organic molecules are concentrated in micro-channels of liquid brine, which favours chemical reactions that produce these nucleotides. However, making other nucleotides and building blocks typically require a higher temperature than that of ice, depending on starting material and reaction pathways, so again we seem to have only addressed another part of the puzzle.

Whether life originated in hydrothermal vents, tidal flats, desert salt pans or deep in the Earth, it had a very limited future there. Far greater supplies of organic chemicals would have been available on the surface. Not only can lighting produce many organic compounds at the Earth's surface (although rather inefficiently, as we saw in the Miller–Urey experiment), but in addition many organic molecules practically "rained down" from the sky during early Earth times from comets and meteorites. But they were spread across the whole Earth, not just one location. So the first microorganisms would have had to adapt to 'eat' this biochemical bounty. This realization led to the idea that the first organism on Earth was perhaps a heterotrophic microbe; an organism using readily available organic compounds for its metabolism. And once the supply of organic molecules was used up with little resupply, life on Earth went through its first major survival crisis, and emerged with two solutions. These were chemoautotrophy (use of inorganic compounds or minerals to get the energy for metabolism) and photoautotrophy (use of light as an energy source). However, most scientists believe today that life on Earth started with autotrophic microbes that drew energy from the conversion of hydrogen and carbon dioxide to methane and water, or fed on other inorganic compounds such as minerals, and built their own organic chemical components.

This makes it hard to test another idea about the origin of life: that it happened more than once. Carol Cleland and Shelley Copley suggested in 2005 the possible existence of a second type of life on Earth, having independently originated from the life we are familiar with, and forming a "shadow biosphere" of life that would be biochemically different from ours. We have not found any life on Earth with a significantly different biochemistry; all terrestrial known life shares the same underlying biochemistry. Is this because this life was the first to appear, the best fitted, or the frozen result of an extremely unlikely event? Or is it because we have just not found an alternative biochemistry in the proposed shadow biosphere? If a shadow biosphere did exist, maybe it is in obscure ecological niches like deep in the crustal rocks or in oceanic floor vents. If so, then there is a good chance we would not detect it. The methods we use to search for and analyse life on our planet, mostly via DNA sequencing and culturing, are specifically aimed at our type of life. It is not difficult to imagine that we could overlook life of a different type even if it existed on our planet.

However, speaking against such a possibility is that life as we know it seems to occupy every habitat and niche on our planet, miles into Earth's crust, at hydrothermal vents, in ice deserts, in tidal pools and oil seeps, among others. A 'shadow biosphere' of life should also be in many diverse places, and we do not see that. There could be two reasons for that. The proposed different forms of life would have competed with each other 4 billion years ago, and only the best adapted or "fittest" organisms would have succeeded and remained. So the reason could be straight competition. Or the survivor could have coopted the most useful chemical functions of the 'looser' into a final, hybrid form which was the ancestor of today's life, just as even today bacteria commonly swap genes between different species and the best-suited genes survive in the overall gene pool. Alternatively, the 'shadow biosphere' could be much better adapted to an environment where the dominant life on Earth has extreme difficulty in surviving. In this scenario the shadow life is hanging on in some place so inaccessible and hostile that we have not even looked there yet. If this is the case, then that life is a tiny minority of all life on the planet.

Whether life originated once, twice or many times, once life appeared and colonized the planet it would have occupied the most favourable environmental niches and eaten any organic compounds around, and hence prevented any other life getting a foothold. The origin of life is a Pulling Up The Ladder event. Once it happened, it destroyed (literally ate up) the conditions which would allow it to happen again.

3.6 Are There Other Planetary Locations Where Life Could Have Originated?

There are scientists that propose that life did not originate on Earth at all, but originated elsewhere and was later transferred to Earth. This idea is known as panspermia and its more modern versions involve the transport of microorganisms between planets in asteroids or comets. It is a distinct possibility and only moves the location of origin, it does not solve it, but other planets might provide a more conducive environment than the early Earth.

Mars is a favourite. Mars has the advantage that an origin of life could have occurred earlier than on Earth, because Mars cooled down faster and did not have the cataclysmic sterilizing impact which produced Earth's Moon. Aside from the timing, the environmental conditions on early Mars were quite similar to early Earth, but with more land and less ocean (and so more shoreline, if that is important, although no over-sized Moon to raise tides on those shores). An origin of life on asteroids and comets seems unlikely, because they don't have an atmosphere which could keep solvents such as water or ammonia liquid for long periods of time at the temperatures occurring on or within these bodies to facilitate the reaction toward larger macromolecules.

An origin in some other solar system can, of course, be hypothesized under quite different environmental conditions than existing on Earth, but the enormous time needed for a rock to travel from one solar system to another makes this seem unlikely. Experiments on spacecrafts show that life can survive in space for tens of years, and we suspect that it can survive for thousands of years in the vacuum of space if it is shielded from UV and X-rays from the Sun. But surviving for the millions of years necessary to travel from one star to another seems very implausible. In addition, even if it did survive, it is very unlikely to hit the Earth. Space is vast, and while solar systems are common they are small compared to the vastness of interstellar space. An asteroid ejected from one solar system is most likely to just drift forever in the darkness between the stars. Even if one did make it to the vicinity of our Solar System, it would most likely pass by or fall into the Sun (by far the most massive body in the Solar System), and not get to Earth. But even if it did get to Earth, the asteroid would still have to survive the fall. Overall, interstellar panspermia seems unlikely.

3.7 Looking for Life

If we cannot say how life originated, nor specify the environment in which it appeared, then can we find life elsewhere? We might gain some indications about the frequency of life by searching for life in our Solar System, which includes eight planets and many moons, some of which are big enough to possibly hold life. And also by looking outside of our Solar System by remotely examining thousands of exoplanets. We have to emphasize that we are only in the very infancy of space exploration and the search for life in the Universe, but a current assessment may be instructive nevertheless. Of the planets in our Solar System, only Venus, Earth, and Mars have or have had oceans on their surface, together with at least some of the environmental conditions that we generally associate with an origin of life. Some of these conducive conditions exist also on the moons of the gas giants, and life, in principle could exist there, for example in the subsurface oceans of Jupiter's moon Europa or in the hydrocarbon lakes of Saturn's moon Titan. Given that environmental conditions on Titan are vastly different from Earth (see also Part III), if life exists there, it is expected to have originated independently from Earth. By contrast to Titan, a discovery of life on Mars may not mean a separate origin of life, as there have been exchanges of meteorites between the two planets. Based on our quick survey of our Solar System we can say that there exist some localities where environmental conditions are present that are conducive to life and even planets that may be inhabited assuming life originated there. So far we haven't found any evidence of extraterrestrial life on these bodies, we only know of life on one world—Earth—but we are only at the very beginning of the search.

What about planets in other solar systems? The number of discovered planets outside our Solar System has now risen into the several thousands and more are discovered every week, but we have even less knowledge about these exoplanets. We can now detect Earth-size planets around other stars, and not only gas giants. Since a fraction of the Earth-size planets might be habitable this also raises the number of potentially habitable exoplanets. However, habitability, the existence of an environment or environments that are conducive to life and the actual existence of life are two different pairs of shoes. The existence of life requires also the origin of life, and the environmental parameters that allow the origin of life are likely much more constrained than just persistence. Persistence is achieved by the incredible adaptability of life through evolution once it has arisen. The question of how much more constrained the environmental parameters have to be for the origin of life looms big if we want to understand its frequency in the Universe. This is pertinent also to the question whether there are alternative routes to the origin of life other than how it happened on Earth. What variations exist on the theme of the origin? Alternative routes and a large amount of variations would certainly increase the frequency of life's occurrence.

3.8 Are We Living in an Empty Universe?

We are stuck in a conundrum about the origin of life on Earth. On one hand, life appears to have originated rather quickly (in geological terms) on our planet after liquid water oceans formed on Earth. We can find laboratory models which support the idea that some aspects of the chemistry of life can occur easily. Many laboratory models of conditions prior to the emergence of life have shown that quite complicated organic molecules can be made under vaguely plausible early Earth environmental conditions. The discovery of many organic molecules such as amino acids, alcohols, trioses, and other biologically relevant molecules in meteorites and in interstellar space attest to the ease with which non-biological chemistry can make them. A range of experiments show some limited patterned replication of protein precursor molecules, nucleic acid-like molecules, and larger structures such as micelles (lipid molecules that arrange themselves in a spherical cell-like form in watery solutions) in completely non-biological systems. Thus, complicated chemistry clearly can happen. On the other hand, life as an integrated whole requires chemistry that is many orders of magnitude more complex than anything replicated in the laboratory, and the chemistry of catalysis, coding and containment has to be integrated to work as a living system. All of these components need to come together at the same place and time to create life. We need a comprehensive theory about how it came altogether, but none is on the horizon.

Our summary from the above discussion is sobering. We don't know how the first organism originated nor in which type of environment, we do not know what type of organism it was, nor when it came into existence. We know only of one origin, but we are not confident that, if there were others, we would know about them. As of 2017, we have no indication that life originated elsewhere in the Solar System or beyond—even though habitable conditions seem abound, but we are only starting our search. Thus, we must acknowledge the possibility that we are rather lonely in the Universe. The initial development of a primitive genetic code and with it the origin of life may be an extremely unlikely Random Walk event, which on Earth occurred rapidly (or, under some hypotheses, occurred elsewhere and then was transported to Earth), but elsewhere may occur only after billions of years, or not at all. Or the origin of life may be a common event and occurring elsewhere very frequently, after a critical innovative step (Critical Path hypothesis). Perhaps, there are even many routes to life (Many Paths hypothesis), and if so, life would be expected to occur even more frequently.

As long as the Earth is the only planet which we know contains life, we have no way of deciding what category of explanation is appropriate for the origin of life, nor of the relative probability of it occurring elsewhere. Life could not appear anew on the Earth today. Today's oxygen atmosphere would not allow the assemblage of needed organic macromolecules, and even without that barrier any primitive prebiotic chemical system appearing today would be a tasty concentration of organic molecules that would be eaten by the vastly more capable and sophisticated life already there. Thus, after life became widespread on our planet and the atmosphere oxygenated, the origin of life became a Pulling-up-the-Ladder event.

Thus, the frequency of the origin of life and how common life is in the Universe, will probably remain one of the greatest unknowns for the foreseeable future. We do not know at present whether the origin of life is a Random Walk event, or follows the Critical Path or Many Paths hypotheses. If the Great Filter is at the origin of life stage, we may live in a rather empty Universe. If it is not, we will argue in the following chapters that we live in a Cosmic Zoo.

Note

1. A video of a modern recreation of the Miller–Urey experiment can be seen at (http://chemistry.beloit.edu/Origins/pages/spark.html).

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4

Using Light: The Invention of Photosynthesis

4.1 Finding Energy for Life

When life started it was likely powered by reactions between chemicals—primarily rocks and gases—that were already present in the early Earth environment. If life originated at hydrothermal vents deep in the sea (as we think is a distinct possibility, as discussed in the last chapter), the volcanic rocks and the gases from volcanic exhalations, such as carbon dioxide and hydrogen, reacted to produce methane and water. Some microorganisms still use this as a source of energy today, and the enzymes that they use for this chemistry appear to be extremely ancient. However, this is a very limited source of energy. There are only a few places on Earth where the crust provides energy for life. Reduced rocks that could react with gases are rare, as they can react on their own (albeit slowly), especially with atmospheric gases. Hydrogen is produced in hydrothermal systems like geysers and sea-floor vents, but these occupy only a tiny fraction of the Earth's surface. Other places where geological energy abounds, such as volcanoes, are so extreme that life cannot survive there. So life can start in such places, but could never spread.

The first step in life's adaptation to a wider world was its ability to use a wider range of chemical sources of energy, and Earth's bacteria and archaea, the most ancient branches of life (Box 1.1), have proven astonishingly good at this. Many different groups of microorganisms have adapted to extract energy from reactions of chemicals in their environment, a lifestyle called chemotrophy, and new environments bring out new groups of organisms. Thus, there are bacteria that thrive in the ponds where nuclear waste is stored,

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bacteria that ‘eat’ plastics and concrete, and bacteria that eat styrene, a toxic side-product of Styrofoam manufacture. Undersea cables have to be sealed not to stop water getting in (their wires are plastic-coated to insulate them), but to stop bacteria getting in and corroding them. Such capabilities have evolved countless times, and such evolution is relatively easy to reproduce in the lab. Recent experiments by Frances Arnold at CalTech showed that only three rounds of mutation and selection could coerce bacteria to make an enzyme that could combine silicon and carbon atoms into a single molecule, making a hybrid material reminiscent of silicone plastics (something that will excite all the lovers of the Star Trek episodes featuring ‘silicon-based life’). So there is no doubt that once life arose it would adapt rapidly to use all the chemical sources of energy available.

4.2 What Energy Can Life Use?

But this is still very limiting. A chemical source of energy is a pair of chemicals that would react given the right conditions. Hydrogen and oxygen are such a pair, reacting to make water. But hydrogen gas does not spontaneously react with air, because to react the atoms in molecules have to be split apart from each other, so they can recombine into a new molecule, and that itself needs energy. Hydrogen and oxygen can be mixed quite safely at room temperature, and will not react. But add energy, in the form of a spark, and the reaction kicks off releasing a lot of energy—the mixture explodes. The term for a reaction that should happen is one that is *thermodynamically favourable* (thermodynamics being the science of energy), but *kinetically inhibited* (kinetics being the study of how fast chemical reactions happen) (Box 4.1).

Box 4.1 Thermodynamics, Kinetics, and Catalysis

Two chemicals will react if two conditions are met, which are summarised by the terms *Kinetics* and *Thermodynamics*. Thermodynamics is the study of how energy drives change, in everything from the molecules to steam engines to the whole Universe. In chemical terms, thermodynamics tells us whether the products of a reaction contain less energy to make than the reactants. If products have less energy than reactants, then energy is released in the reaction, often as heat; thermodynamics says that this is a reaction which can happen spontaneously. The energy concerned is called Free Energy, meaning energy that is available to do useful work. Heat is not Free Energy, which is why heating ashes up does not make them go back to being wood.

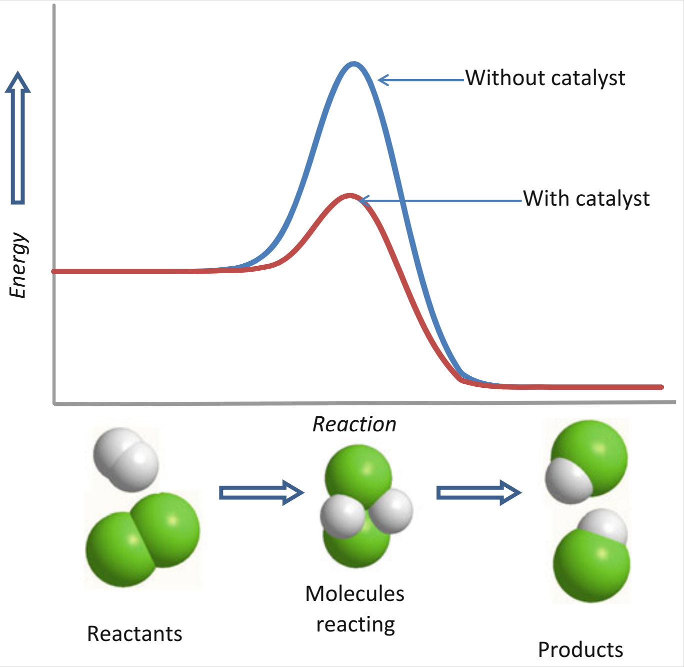
(continued)

Box 4.1 (continued)

Thermodynamics does not say how fast a reaction will go. The speed of reaction is the realm of Kinetics. To react, atoms or molecules must come together, but they must also be re-arranged to form new molecules. Rearrangement almost always involves bending, stretching or breaking bonds between atoms, and that takes energy. Usually that energy comes from the energy of movement of the molecules—as they smash into each other their bonds are bent a bit, and occasionally they are distorted enough to react. Heating a substance up therefore both speeds up collisions and makes them more energetic, making reactions happen faster. This is why pressure cookers can cook your vegetables in a few minutes.

So a chemical reaction can be *Thermodynamically favourable* but *kinetically inhibited* if energy would be released if the reaction happened, but it happens infinitesimally slowly.

These energies can be summarised in a reaction diagram like this.



The vertical axis shows the energy of the reaction as a whole, and horizontal axis shows how far the reaction has progressed. At the start the reactants have some energy, they need some more to react, but in the end they have less energy, i.e. energy has been released. The hump in the middle is called the Activation Energy, and if it is too high then the molecules do not have enough thermal energy to get over it, and the reaction is *kinetically inhibited*.

(continued)

Box 4.1 (continued)

The other way to make a reaction to happen is with a *catalyst*. A catalyst works by making the molecules in the 'twisted' intermediate stage more stable, so that it needs less energy to make the molecules react—the Activation Energy is lower. Enzymes are spectacularly efficient catalysts, which is why life can make reactions happen that are thermodynamically favourable but kinetically inhibited.

What life can do is take the chemicals of the kinetically inhibited reaction, and catalyse that reaction in a way that captures the energy released. Catalysis increases the rate of the chemical reaction without the catalyst being used up. Thus, the catalyst can repeatedly accelerate the reaction even if present only in very small amounts.

Other things can catalyse the reaction of hydrogen and oxygen as well. Heating up the molecules, ultra-violet light of the right wavelength, the presence of some metals such as nickel or platinum, these all can all kick off the reaction. In general, any reaction that is *kinetically inhibited* can be started by enough heat, and often there exist mineral catalysts that can also make the reaction happen fast. So chemotrophic life is dependent on the presence of chemicals that meet all three criteria: they can react with each other to release energy, and that reaction is *kinetically inhibited*, and there is no natural catalyst or other trigger such as heat or light to make the reaction happen anyway. This is quite an unlikely set of circumstances, occurring mostly where volcanic activity has brought material from the Earth's mantle close to the surface. So life that is reliant on chemotrophy will be very limited in extent and in mass. What other sources of energy are available?

Life cannot use all forms of energy. Some are just too powerful. Nuclear decay is such a source of energy. Decay of radioactive isotopes in the mantle and core are the main power for Earth's magnetic field, for plate tectonics and volcanism. But the radiation given off by decaying atoms will destroy organic molecules. This is why such radiation causes mutations. So direct capture of the energy of nuclear decay is implausible.

Energy can also be too weak. In theory, you could power an organism with tidal energy. But although there is a lot of energy in tides, as man-made tidal power schemes show, the energy is too diffuse, spread out over kilometres of ocean. Magnetic energy is also too weak of an energy source on Earth, although in other planetary scenarios alternative energy sources may be a possibility, for example magnetic energy being harvested by life on a planet that orbits a neutron star or a magnetar. Living systems extract energy from processes or reactions in steps or quanta, and collect them to build high energy molecules like ATP. Thus the energy must be concentrated into a single molecule (or connected system of molecules) to be used.

There seems to be a minimum amount of energy in a step, called the Biological Energy Quantum (BEQ) that life can use to build high-energy molecules. In theory a long, thin organism growing on the sea floor could use the temperature difference between its sun-warmed top and its ocean-cooled base to drive reactions. Temperature differences can be used as a source of power; this is how a digital thermometer works, detecting the tiny voltages generated by temperature differences between two metals. But the amount of energy per molecule that can be extracted from these sources is tiny, far below the BEQ.

4.3 Using Light

So some energy sources that we, as technological creatures, can use are not available to non-technological life. But one source is abundant, available, and has the right ‘voltage’, and that is sunlight.

A key step in the evolution of life was the evolution of the ability to capture sunlight and use its energy to drive chemical reactions, enabling life to transcend local geochemical energy sources. Light is a stable, abundant, dense source of energy, readily available on the surface of any terrestrial planet. Without the ability to capture light and convert it to chemical energy, life would be confined to a few, isolated environments, and more importantly would not be able to build up the large biomass of the Earth today. It is estimated that the total amount of geothermal energy on the Earth is about 0.2% of the energy of sunlight falling on the surface, and only a small fraction of that geothermal energy is turned into chemicals that life could use. Using light to make biomass, a process called photosynthesis, ultimately enabled a 500-fold expansion of life on Earth.

When we talk about organisms that use light, we naturally look out of the window and see trees and grass. Land plants, oceanic cyanobacteria and algae are the dominant photosynthesisers on Earth. Their photosynthesis is called oxygenic, because as a byproduct it makes oxygen. But in biochemical and evolutionary terms, capturing light and making oxygen are two completely different things. This chapter is about capturing light alone. We will discuss making oxygen in the next chapter.

How often did that ability to capture light appear? There are several lines of argument that suggest this complex process follows the Many Paths model, and hence is inherently likely to occur. Lynn Rothschild, astrobiologist as NASA, comments that all terrestrial planets have abundant surface light and surface carbon, and so are likely to evolve a way to use that light to capture that carbon, but we can go one better, because not only has this happened once on Earth, it has happened at least twice, and maybe as many as four times.

The vast majority of light capture on Earth is performed by organisms that use the pigment chlorophyll to capture photons. Chlorophyll was only 'invented' once in evolution. The diverse organisms that use chlorophyll all make it using enzymes that are descended from a common ancestor (see Box 4.2 for a short summary on how we know this). The biochemistry that makes chlorophyll is complicated, but is in part similar to the biochemistry that makes haeme, the iron-binding molecule that (among other things) makes the red protein (haemoglobin) in our blood (Fig. 4.1 and Box 4.3).

Box 4.2 Common Ancestors

How do we know how ancient a protein is, such as an enzyme, and whether it evolved just once? Modern molecular biology provides methods that can be used in two ways to address this. Both are based on knowing the sequence of amino acids in a protein (usually by finding the sequence of bases in the gene that codes for that protein, as this is much faster and cheaper). The structure of a protein, and hence its function, is determined by its sequence, but many different sequences can result in proteins with the same function. As organisms evolve, the sequence of their genes and proteins gradually changes as the genes mutate, so no two organisms have exactly the same genes. But if they are closely related, their DNA will be almost identical. The further apart they are on the evolutionary tree, the more different their genes will be. So if we find two proteins that have the same function *and* similar sequences, we can be confident that they evolved from a common ancestor protein. If we look at all the proteins that carry out a specific function, for example making chlorophyll, and they all have similar sequences, then we can be confident that they all evolved from one, single ancestor, and so that this particular protein function was only invented once. Equally, we can track the evolution of whole organisms that way, and see how related they are (that is one way that we know that fungi are more closely related to animals than to plants). If we find a protein in one group of organisms and no other, then we can be confident that protein appeared in the common ancestor of those organisms, and so probably only occurred once.

This type of inference gets harder as we look further back in time. The proteins of humans and chimpanzees are almost identical, because we share a common ancestor living about 5 million years ago. The genes of archaea and humans are extremely different, and seeing that there is still more similarity between them than you would expect by chance (and hence that humans are more closely related to archaea than to eubacteria) requires some sophisticated software, very powerful statistics, and some considerable expertise.

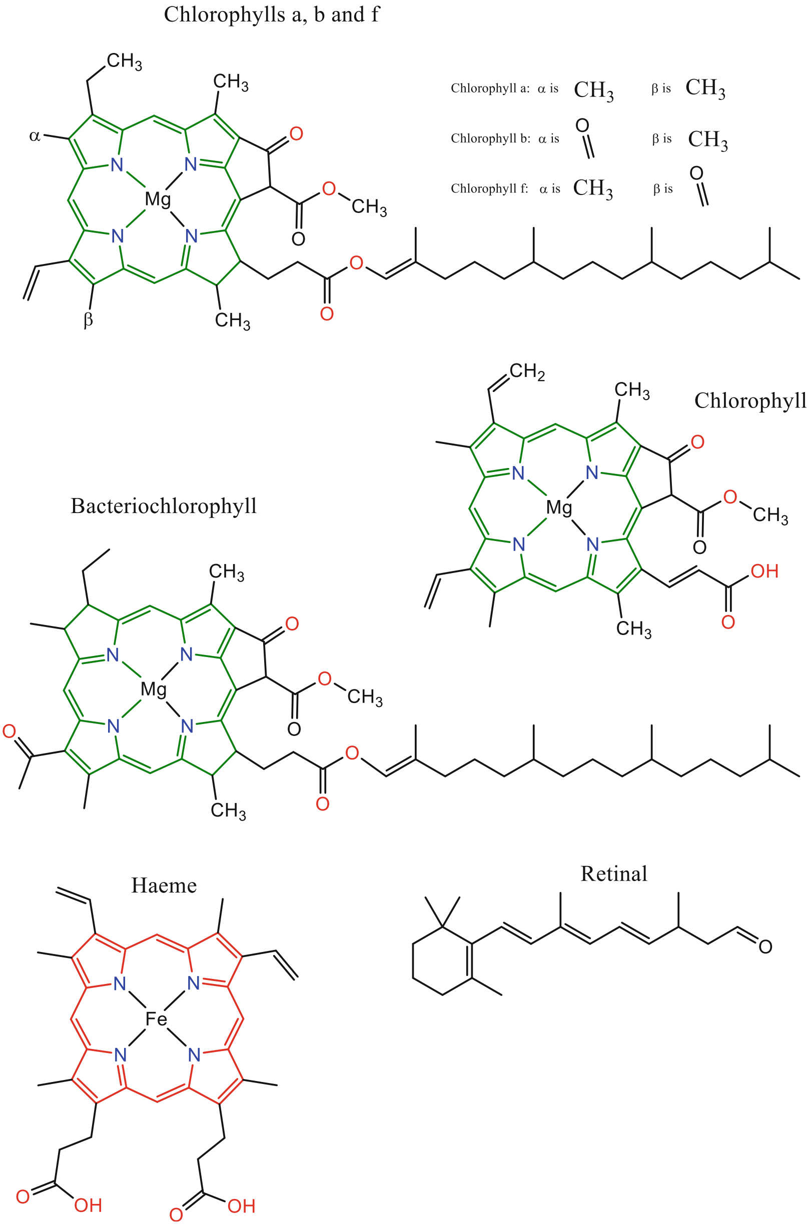

Chlorophylls a, b and f
Chlorophyll a: α is CH3 β is CH3
Chlorophyll b: α is O β is CH3
Chlorophyll f: α is CH3 β is O
Chlorophyll c
Bacteriochlorophyll
Haeme
Retinal
Mg
Fe
N
O
OH
CH3
CH2
α
β

Fig. 4.1 Structures of some pigments used by life. The chlorin ring in chlorophyll a, b, c and f and the bacteriochlorin ring in bacteriochlorophyll is coloured *green*. The central ring in haeme, called a porphyrin ring, is coloured *red*. There are many different haeme types—only Haeme B, one used in the red haemoglobin pigment in animal blood, is shown here. Retinal, another pigment, to capture light has a quite different structure (see also Box 4.3)

Box 4.3 Variations on Chlorophyll

"Chlorophyll" is actually the name for a group of molecules with the same central ring, the chlorin ring, but a variety of different side-chains. The most common one, Chlorophyll-a, found in green plants, absorbs light in the violet to blue and orange to red region of the spectrum. Chlorphyll-b is also common in plants, and absorbs redder light than Chlorophyll-a. Chlorophyll c, which also absorbs in part of the blue spectrum, is used by marine algae such as diatoms, brown algae, and dinoflagellates. Chlorophyll-f can absorb energy from near infra-red light (the wavelengths that TV remote controllers use). Bacteriochlorophyll has a very similar structure, and is used by non-oxygenic photosynthetic bacteria (see Fig. 4.1 for structures).

The structure of the chlorin ring is similar to that of the porphyrin ring which is found in Haeme, the coloured component of the oxygen-carrying protein haemoglobin in our blood. However haeme has an iron atom in the middle, not magnesium (Fig. 4.1).

Other pigments used to capture light have quite a different structure, such as retinal used in bacteriorhodopsin, and also in the rhodopsin pigments that sense light in our eyes.

Chlorophyll-based photosynthesis evolved early in the evolution of life. By 3.5–3.2 billion years ago the fossil record shows stromatolites, fossilized columns of bacterial mats that are exactly like those growing in warm, shallow lagoons today. They grow in columns because the bacteria in the top layers are using sunlight to build up biomass. When those organisms reproduce, the ones that are buried die, and are eaten by deeper layers of microorganisms that do not require light. Trapped sand and silt make the whole structure solid.

For green plants, the green pigment chlorophyll is one key part of the photosynthetic apparatus. The other is the Reaction Center (RC), which takes the light energy captured by chlorophyll and transforms it into chemical energy. It is the RC that is the key innovation. Capturing light is easy. Every coloured pigment in an animal, flower, fungus or bacterium is capturing light. But the energy of the light that falls on coloured pigments (even the pigments of this book, if you are reading a hard copy) is converted just into heat energy, which goes to warming the animal or plant up. It is usually not put to useful work. It is the RC that transforms the light energy into work. The evolution of chlorophyll and the RC freed life from chemical sources of energy, and allowed it to spread over the planet.

Chlorophyll and the RC are not the only part of the machinery of photosynthesis. Surrounding the chlorophyll molecules are other pigments called

Antenna complexes. They capture more light, and pass that energy to the central chlorophyll molecule. The pigments in the Antenna complexes seem to have been adopted from different molecules in different species, and so their evolution follows a Many Paths process. The complex membranes in which photosynthesis occurs in all organisms now also seem to be elaborations of simpler membranes that can be seen in microfossils of the earliest photosynthesising bacteria known, and again seem to have evolved easily. It is the evolution of chlorophyll and the RC that were the critical steps to the photosynthesis carried out by almost all life on Earth today.

Once life found a way to capture light, it could literally expand its mass, allowing the large, complex ecology that would itself permit complex life to evolve. Capturing light energy allowed life to spread to any place that can sustain even the smallest amount of liquid water. Photosynthetic organisms have been found that harvest light in some very unexpected places, like inside rock crystals in the Atacama desert of Chile or in the valleys of Antarctica. Photosynthetic organisms have even been found harvesting the light from the glow of deep sea volcanic vents, miles below the surface where no sunlight penetrates. As a source of energy, light is too useful to be allowed to go to waste.

So was photosynthesis a unique, Random Walk event? We think not, because although chlorophyll-based photosynthesis has arisen only once, the ability to capture light energy itself has arisen at least one more time, and possibly three more times, completely independently.

4.4 Other Paths to Using Light

Reading this book, you are using a light-capture mechanism completely different from chlorophyll. In the retina of your eye, proteins called rhodopsins, each tuned to different wavelengths of light, capture photons of light and turn their energy into chemical energy. That chemical energy activates other proteins to trigger nerve impulses, which your brain interprets as the sensation of “sight”. Your eyes are capturing light energy, but not using chlorophyll—they use rhodopsin instead.

Plants also have special pigments to detect light. The photochromes are a set of detector molecules that are a combination of protein and a pigment distantly related to chlorophyll called a bilin. They also absorb light and turn it into chemical energy, but do that only when they detect light falling onto them, not to make more plant material. They are used to tune the plant’s natural rhythms to the day-night cycle, for example so that it is ready to start photosynthesising when the Sun rises. Plants also share a third type of light detector with animals, a series of proteins called cryptochromes—these have yet another pigment in them, a flavin molecule (related to riboflavin, also known as vitamin B2) which is chemically unrelated to the chlorophylls or the pigment in rhodopsin.

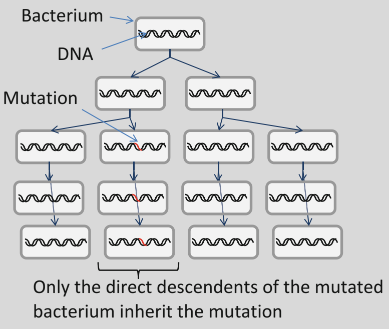
However, what makes rhodopsin special is that it is not just used to detect light. The rhodopsin in bacteria is called (logically enough) bacteriorhodopsin. Bacteriorhodopsin-based light capture is chemically completely different from chlorophyll-based capture. Like the rhodopsins in our eyes, most bacteriorhodopsins are used to sense light, but a variant called proteorhodopsin has been found that is used by many marine microorganisms to capture energy for general metabolism, just like chlorophyll-based systems. Bacteriorhodopsin is also used as a supplementary energy source for some halobacteria, which are microorganisms that live in salt-rich environments such as the Great Salt Lake in Utah or the Dead Sea in Israel.

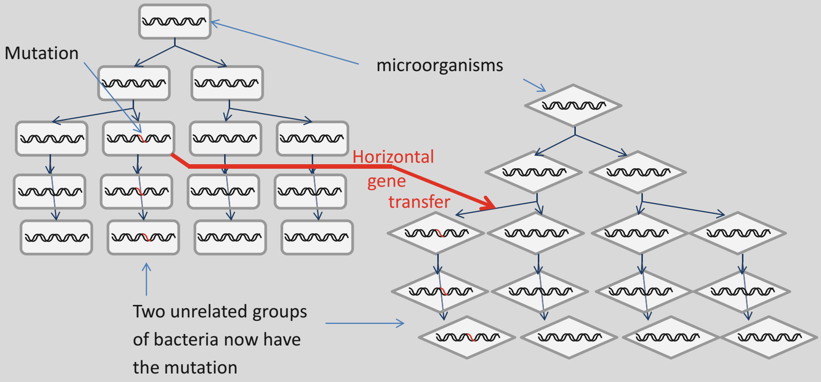
The microorganisms that use bacteriorhodopsin cannot survive on light as a sole energy source (as plants can), but need some additional chemical energy to live and grow. The marine bacterium SAR11 (the smallest free-living organism currently known) captures light energy using proteorhodopsin, although it seems to use this to supplement other sources of energy, mostly eating other organisms or their remains. SAR11 is a common organism: Stephen Giovanni from Oregon State University estimates that 25% of all the bacteria in seawater (by number, not by mass as they are tiny) come from the SAR11 clade. This is not an oddity, this is a major alternative form of light capture.

Bacteriorhodopsin uses the chemical retinal as its photon-absorbing pigment, and transduces the energy of a photon to move a proton across a membrane, generating a membrane potential (in effect, a voltage) that can then be used to drive chemical synthesis. It is not powerful enough to power the production of oxygen (we will get to oxygen in the next chapter), but it nevertheless plays a major role in the marine ecosystem. Bacteriorhodopsins evolved in bacteria, but have crossed over into eukaryotes by horizontal gene transfer (Box 4.4), where, in at least the case of the single-celled eukaryote *Oxyrrhis marina*, it is used inside the cell in a specific membrane system that may be a special energy-capturing organ like a chloroplast in a plant. This is odd, as *Oxyrrhis marina* is a microscopic predator—its normal lifestyle is to eat other organisms. It seems to have acquired this simpler form of photosynthesis as a backup.

Box 4.4 Horizontal (or Lateral) Gene Transfer

The exchange of genetic material between different genomes, most commonly occurring between bacteria, but also between unicellular and multicellular organisms. Genetic material is either exchanged during a temporary union between two cells (conjugation), transmitted from one cell to another via a virus (transduction) or acquired as free fragments of DNA within the environment (transformation). The new genetic material is then inserted between existing genes of the host cell or a regrouping of genes occurs in which old and new DNA segments are edited and combined. Horizontal gene transfer is distinct from vertical gene transfer, in which genes are transferred from the parent to the offspring.


Vertical Gene transfer (inheritance)
Bacterium
DNA
Mutation
Only the direct descendents of the mutated bacterium inherit the mutation


Horizontal gene transfer

These two types of light energy capture are very widespread, and very well known. Two others are rarer and more controversial, but we think the case for them is strong, and they illustrate that there are Many Paths to the use of light to power chemistry.

An extraordinary example of the evolution of the ability to capture light is the case of the pea aphid, *Acyrthosiphon pisum*. This small sap-sucking animal has acquired the genes to make the red and orange pigments called carotenoids (after carrots, which have a lot of them) that are usually found in plants. Usually such genes would just be used to colour the animal, but in this case the aphid can sometimes accumulate them inside its abdomen, and use the pigments to capture light energy, and transform it into chemical energy that the cell can use. They are authentically carrying out the capture of light energy to support their metabolism. Even though the most common form of light capture, based on chlorophyll, only evolved once, the function of capturing light to drive chemical reactions seems to have evolved at least three times independently. How did it evolve?

The most compelling idea is that photosynthesis evolved from mechanisms that were meant to *protect* organisms from light, and particularly from harmful UV radiation. To protect an organism from UV, the protection system has to absorb the UV photons; that means a pigment. However, when a pigment molecule absorbs a UV photon the energy of the photon boosts the electrons of the pigment molecule into an excited state. Such excited states are potentially unstable, and the excited pigment molecule would normally pass its energy quickly on to another molecule, damaging that other molecule or reacting with it (this is what damages your DNA when it absorbs UV from sunlight—if you are lucky the result is sunburn, if unlucky, skin cancer). The protection system must isolate that excited pigment until it can lose that energy safely as heat. This can be achieved by a combination of pigment and "protecting" protein(s) that keep it away from other molecules with which it might react. From this mechanism, 'all' life has to do is evolve a mechanism whereby the protective protein(s) can take some of the energy away from the pigment and pass it to an enzyme that does the chemistry that life needs.

Intriguingly, there are modern examples of organisms that have UV protection mechanisms that may be part-way along this path to evolving a method of passing some of the energy of that UV light on to useful chemical reactions. These are 'missing links' between organisms that only try to defend themselves against UV and ones with efficient, highly optimized light-capture systems. These are the melanised (dark-pigmented) fungi. Some fungi defend themselves against UV by surrounding themselves with walls heavy in the pigment melanin (similar to the pigment that makes animal skin and hair dark, including our own). In their native environment this is probably to protect against UV, but it also protects against ionizing radiation, and the walls of the damaged reactor core of the Chernobyl nuclear plant have been colonized by such fungi.

Some of these melanised fungi are found to actively grow toward particles of radioactive matter, and even towards sources of radiation, something that makes little sense if the fungi do not actively use the radiation in some way. In addition, some of these fungi also grow better under a modest level of radiation, suggesting that they are gaining benefit from what is usually dangerous. Ekaterina Dadachova and her colleagues suggest that the fungi are actually using that radiation as a source of energy. They claim that the cells do not just use melanin to adsorb the energy of radiation, but also convert a part of it into chemical energy in the cell. The fungi are capturing energy from light, albeit very inefficiently compared to 'true' photosynthesizers. So this is a fourth example of the capture of light energy (in this case UV light) to provide chemical energy for life independently invented.

Evolution of photosynthesis is not without its dangers. The ability to capture light and use it carries with it the risk that the electrons being moved around between pigments and other molecules will 'leak' and damage other components of the cell. And only light of a particular wavelength has the energy you need. Chlorophyll absorbs yellow and red photons (this is why it looks green—it lets the green ones through). That is enough energy to power photosynthetic reactions, although for green plants there is another step involved as we will discuss in the next chapter. But the quantum mechanics that allow chlorophyll to absorb red light means that it also absorbs light of twice the energy as red, which is blue light. What happens to the surplus energy? In the worst case, it also leaks out of the chlorophyll molecule and causes chemical reactions in anything nearby. Thus, photosynthesisers are unusually sensitive to damage by blue light, and must protect themselves from it (by contrast melanin absorbs almost all wavelengths, which is why it is brown or black, and usually just turns the energy into harmless heat). So there are other steps to photosynthesis than evolution of a pigment and a way of capturing its excitation to perform chemical reactions. Despite this, the ability to capture the energy of light has evolved independently at least two times (chlorophyll-based in plants, rhodopsin-based in bacteria), and arguably four times if we include the light-capturing aphids and melanising fungi, through completely different and independently evolved mechanisms, and those are just the examples that we know of. We argue therefore that this is a Many Paths process, one that will arise readily on any planet where life appears and can receive light from its parent star.

4.5 Using Energy

However, we have skipped a step. What is light energy *used for*? Organisms use energy for two types of purpose—to maintain themselves and to grow. Just being alive takes energy. If an active organism cannot acquire this basic level of energy, called the Maintenance Energy, then it must either form a dormant state like a spore or it will die. Most microbial species can form spores, as can many fungi and simple plants like mosses, even some animals like "water bears" (tardigrades) can form dehydrated, dormant forms called tuns. However, more complex plants cannot—seeds are still active and will not last indefinitely—and most animals cannot either. So for them, a constant energy supply is important.

However, this is just staying alive. The main reason that green plants capture sunlight is to grow, and that means capturing carbon from the environment and converting it into plant matter. On Earth carbon is available as carbon dioxide (or carbonate rocks, its mineral equivalent). So the photosynthesis reactions of green plants are used to power the conversion of carbon dioxide into biomass. The reactions used to capture carbon dioxide into biomass (called 'fixing' the CO_2) are called the *Dark Reaction* of Photosynthesis, as they can continue in the dark using energy stored up during the day. The actual capture of light energy are the *Light Reactions*, and of course can only happen when there is light.

Carbon dioxide (CO_2) is a very stable and chemically quite unreactive molecule (this is why CO_2 is used in fire extinguishers; if doused onto a fire it reacts with almost nothing even at red heat). It is unreactive for two reasons. CO_2 is thermodynamically stable—it is the most stable combination of carbon and oxygen atoms there is, and one of the most stable carbon compounds there is, so you have to put in a lot of energy to turn CO_2 into anything else. It is also kinetically stable. The bonds in CO_2 are strong, and take a lot of energy to break, no matter what the end product of the reaction might be. Despite this, life has found six different ways to capture carbon dioxide into organic matter, of which one, called the Calvin Cycle, is used in green plants. The others are used in different photosynthetic or chemosynthetic bacteria. There are in total 23 enzymes that could, in principle, be used by life to capture carbon dioxide into biological material. Clearly, acquisition of the ability to use energy to capture CO_2 is a Many Paths event, evolving from different starting points in many organisms.

One trick life has used several times is not to use carbon dioxide directly, but to use bicarbonate ions, which CO_2 forms when it dissolves in water.

Bicarbonate is still thermodynamically stable, but it is much easier to break the bonds in a molecule of bicarbonate. And life has even evolved an enzyme (carbonic anhydrase) to catalyse the conversion of CO_2 into bicarbonate. In fact, it has evolved it several times. Some picoplankton have no carbonic anhydrase at all, suggesting they have evolved a completely different mechanism for mobilizing CO_2, again speaking to the Many Paths evolution of the *Dark Reaction* part of photosynthesis.

Would life on other worlds use light energy to capture carbon? The many ways that life has found to capture CO_2 suggests life would find solutions to carbon capture on a world like Mars or Venus with a CO_2-containing atmosphere (if they are not uninhabitable for other reasons). But what of other worlds in which carbon is not present as CO_2? One of us explored the possibility of a world where the atmosphere was mostly hydrogen and carbon was present as methane. We found that not only is carbon capture easier on that world than on Earth, but that there were Earth enzymes already known in terrestrial bacteria that carried out all the key steps of a methane-capturing photosynthesis.

Thus this key innovation, the ability to use sunlight to power the chemistry of life, and to use that power to capture carbon from the environment to build more life, is a Many Paths process. Carbon capture has evolved many times, and the ability to capture light has evolved at least two times using completely different mechanisms, and may be evolving today a third time in aphids and a fourth time in the melanized fungi. This step on the path to the Cosmic Zoo is likely to be common.

But we have skipped over one aspect of photosynthesis. As we mentioned at the start, nearly all photosynthesis on Earth is carried out by green plants, algae (such as seaweeds), and a group of bacteria called cyanobacteria known for their green colour. These green organisms all produce oxygen. Together they constitute more than 99% of the photosynthesizing organisms on the planet. Is there a unique bottleneck in life's development of a large, complex ecosystem in the appearance of oxygen-producing green plants? We will explore this in the next chapter.

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5

Oxygen: From Poison to Photosystem II

5.1 All I Need Is the Air That I Breath . . .

Oxygen in the air is essential for animal life, especially our own. A healthy adult human can go 2 weeks or more without food, several days without water, but no more than 5 minute without oxygen before he or she suffers irreversible damage. Every schoolchild knows that green plants use the energy of sunlight to make the oxygen that we breath. The making of oxygen, a process called oxygenesis, is seen as being of central importance to the development of complex life. Without oxygen, none of today's complex animals could survive, from corals to camels. Donald Canfield says that "The evolution of oxygen-producing cyanobacteria was arguably the most significant event in the history of life after the evolution of life itself". And yet in the last chapter we did not mention oxygen at all. Why?

This is not as odd as it seems, because capturing light energy and using that energy to make oxygen are, evolutionarily and chemically speaking, two very different topics. The ability to capture light energy has evolved many times, and we are confident it would evolve on other worlds. But the ability to harness that energy to make oxygen only happened once on Earth. So we need to talk about that separately.

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5.2 Why Make Oxygen?

One of life's major uses for energy is to capture carbon from the environment, where it is present mostly as CO_2, into biological matter. This requires reducing the CO_2, which requires transferring electrons to it, and those electrons have to come from other chemicals in the environment. Early photosynthesising life probably got its electrons from a range of environmental chemicals that are relatively easy to oxidize, that is to say, give up their electrons easily, like iron salts or hydrogen sulphide. Microorganisms that can perform this sort of photosynthesis are known today, and are called anoxygenic photosynthesisers because they use chlorophyll to capture light energy and build biomass, but they do not make oxygen.

As we discussed in the last chapter, the evolution of photosynthesis liberated life from geochemical sources of energy, but anoxygenic photosynthesisers still need a chemical they can oxidize. Swimming in the sea, the most common ions that could be oxidized are chloride and bromide, but they are strong oxidizing agents themselves and it therefore takes a lot of energy to extract electrons from them. Johnson Haas at Western Michigan University has suggested that a form of photosynthesis that uses chloride as a source of electrons could have evolved on Mars, where water is very scarce and chloride salts in the soil are common, but life on Earth had another more plausible alternative, and that was to get electrons from the most common chemical available to any organism living in water—from water itself.

Most photosynthetic life on today's Earth (by mass) uses water as a source of electrons, and that life makes oxygen gas as a waste product. It makes oxygen even though there are two major drawbacks of doing so. The first is that splitting water to make oxygen requires a great deal of energy, much more than is captured by a chlorophyll molecule. How that approach still can work in producing oxygen we elaborate on later. The second problem is that making oxygen is dangerous, a problem which we address first.

Oxygen gas in our atmosphere is relatively unreactive, but the molecules formed on the path from water to oxygen gas by any route are extremely reactive, and readily destroy biological molecules. These are called Reactive Oxygen Species (ROS), and as their name implies, they react very readily with many molecules in the body, damaging them beyond repair. ROS damage is a substantial part of what makes you age. So making oxygen requires cells to make a whole array of proteins to defend themselves from oxygen, and making that cellular machinery slows down their growth. Protecting ourselves from these Reactive Oxygen Species is a substantial part of the biology of organisms that use oxygen in their metabolism, as we and plants both do.

However, the great advantage provided by oxygenesis is that it frees life from the need to find rare chemicals such as sulfide, hydrogen or iron. Suddenly organisms can grow anywhere where there is water and sunlight.

5.3 The Great Oxidation Event

Oxygenic photosynthesis—the use of light energy to capture CO_2 and produce oxygen—seems to have exploded on the biosphere about 2.4 billion years ago. Thick layers of carbonate rocks, rocks made from the remains of bacteria that were deposited on the sea floor at that time suggest that this was a major productivity breakthrough for the biosphere. This short time in geological history is called the Great Oxygenation Event (GOE). From then on Earth's atmosphere contained a significant amount of oxygen, maybe as much as 1% (still low compared to the 21% today, but critical to the chemical evolution of the Earth). Before the GOE, reduced rocks from volcanoes were stable on the surface, and methane from life and hydrothermal vents could stay in the atmosphere for months, providing a potent greenhouse effect. After the GOE, reduced rocks were spontaneously oxidized by atmospheric oxygen, and methane was consumed both by life and by reaction with the molecular oxygen in the air. The very surface chemistry of the planet changed, and the chemistry of life had to change with it; today, organisms that can live only in reduced environments (obligate anaerobes) are found in only a few refuges where once they dominated the planet (we will discuss the impact of that extra 20% of oxygen in Chap. 9).

However, this was not when oxygenesis evolved, only when it took over the biosphere. While today green plants are the most obvious oxygen producers, until about 1 billion years ago the only organisms generating oxygen on the Earth were bacteria called cyanobacteria. There are some fossils that look like cyanobacteria that were found in rocks dated to well before the Great Oxygenation Event. Despite this antiquity, all oxygenic photosynthesizers use the same molecular mechanisms to capture light energy and split water, which suggests that this mechanism only evolved once.

Was the evolution of oxygenesis a Random Walk event, a highly unlikely process that luckily occurred on Earth, or a Many Paths process that could occur by multiple routes on different worlds? As we have only the one event to guide us, we cannot know, but we can dig into how oxygenesis might have evolved on Earth to guess how often the components of oxygenesis arose, and so how likely it is that they could arise elsewhere.

5.4 How to Make Oxygen

There are two problems life must overcome to use water as a source of electrons, generating oxygen. The first is that a single photon of visible light does not provide enough energy to split water (if it did, sunlight would destroy our oceans). So life has to add up the energy from at least two photons to split one molecule.

We know how life does this today. Cyanobacteria take two photosynthetic systems, each of too low a power to split water, and hook them in series to add their energies. One photosystem is adapted to become highly oxidizing, the other highly reducing—together they take two photons of light and use them to split one electron from a water molecule. The traces of the evolutionary process that created two systems from one are still left in the cyanobacterial genes. Duplication—making two systems from one common ancestor—is a common evolutionary strategy. Genes that code for one protein are duplicated, and then the two copies are selected for slightly different functions. An example in your genes are the haemoglobin proteins (Fig. 4.1, the red pigment in your blood), the proteins that make up the lens of your eyes, and the many forms of collagen that give skin, tendon and cartilage their characteristic strength and flexibilities. All are families of genes evolved by gene duplication.

We should note here that green plants use the same process to split water and make oxygen as do cyanobacteria. However, this is not an independent invention of oxygenesis. We will discuss how they came by that ability in the next chapter. For now, we can just note that they got the ability from cyanobacteria.

However, evolving those newly duplicated genes to solve the chemical challenges of making oxygen from water was hard. The challenges to evolving this metabolic pathway are

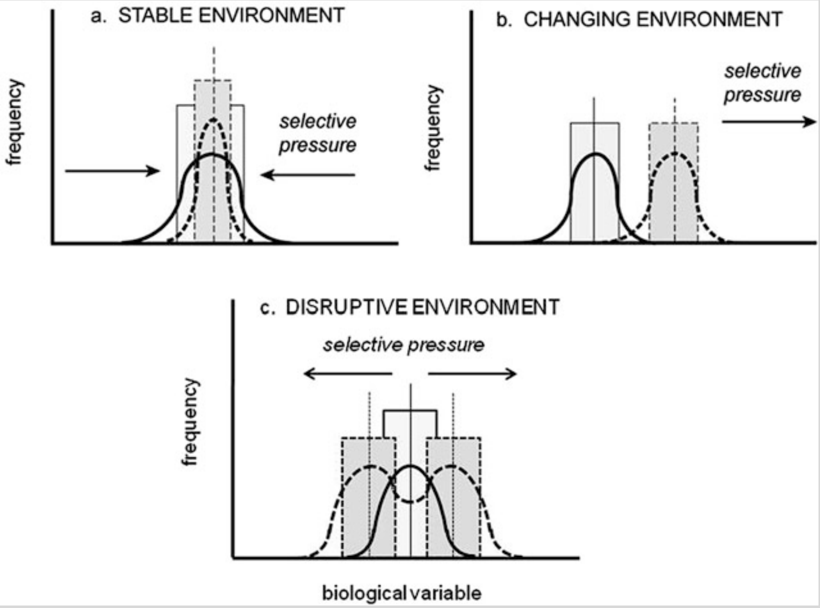
1. That two water molecules must be split to produce one molecule of O_2, while at the same time handling four electrons (and four protons to balance their charge). This is a feat of molecular synchronization that must be completely accurate, or the electrons will end up in other molecules and destroy the photosynthetic apparatus

2. The two photosynthetic systems (called PS-I and PS-II) must be tuned to the right “potential”. Specifically, PS-II must be shifted to a strong positive (oxidizing) potential while PS-I is shifted to a highly negative one.
3. The original, anoxygenic photosynthetic system was highly sensitive to oxygen—the smallest whiff of oxygen would destroy it (this is still true of some anoxygenic photosynthesisers today). The oxygen sensitive components of an anoxygenic photosynthetic apparatus had to be transformed into oxygen resistant ones.

There are several hypotheses how these problems were overcome and hence how the transition occurred.

One idea that we like says that the ability to produce oxygen arose from an ability to defend against it, just as it is believed that photosynthesis itself arose from an ability to defend against the damage caused by light (see Chap. 4). Even before oxygen became common on the Earth’s surface, Reactive Oxygen Species such as hydrogen peroxide were not unknown on the planet. There was no ozone layer in those days (ozone comes from the high concentration of oxygen in our atmosphere), so the amount of UV radiation reaching the surface would have been much higher than today. UV light can split water into reactive species such as hydrogen peroxide, which is a powerful sterilizing agent. The earliest oxygenic organisms may have evolved from bacteria living in small bodies of fresh water, where UV light could penetrate all the way down to the bottom of the pond. An ability to protect yourself from oxidizing chemicals would have been useful to such bacteria (meaning that it would be a positive trait for natural selection, see Box 5.1), and an ability to conduct photosynthesis in their presence would have been especially valuable. So Point 3 above could have evolved in many places. An easy way to get rid of hydrogen peroxide is to convert it to the (relatively) unreactive oxygen gas—the ability to do that solves a lot of Point 1 above, and this ability has also evolved independently several times. So there are plausible stories we can tell, but we must admit that this is speculation.

Box 5.1 Natural Selection and Selective Pressure



Frequency (number of individuals within a population) is plotted against a biological variable (physical or physiological trait). The vertical line shows the populations' mean, the solid lines of the bell curves the standard deviations of the original populations, and the dashed lines the standard deviations of the descendent populations. (a) When stable environmental conditions prevail, mutations, genetic recombinations, and genetic drift tend to be selected against, because a larger number of individuals (frequency) with traits closer to the mean value will survive and reproduce in greater numbers. The optimal adaptation to the selective pressure will remain the same resulting in the same mean but in a reduction of the variance. (b) When an environmental feature shifts in a particular direction (say the average habitat becomes warmer), the individuals that are at one side of the bell optimum (say those that have a thinner fur) have an adaptive advantage. The result is that the mean value for the trait will shift in the favored direction to accommodate the change as more of these individuals survive and produce offspring. (c) New species commonly arise when a previously homogeneous environment splits into new environments that change in different directions. The populations then adjust to the selective pressures in their new environments, respectively, with the result of two bell-shaped curves, each one being optimized for its new environment (modified from Irwin and Schulze-Makuch 2011).

It is also likely that those early photosynthesisers found it useful to make oxygen. Oxygen is poisonous to organisms that are not adapted to it, and 2.5 billion years ago only very few organisms would have been able to handle it. So if an organism evolved a way to make oxygen, it would have a powerful chemical weapon to kill competitors in its environment. Even small amounts of oxygen might have sufficed. In addition, it would have also oxidized the sulphide and iron in the environment, robbing competitors of the ability to carry out anoxygenic photosynthesis. Defence against oxidative damage becomes the ability to use Reactive Oxygen Species as a weapon, and that becomes the ability to use those same reactions as a source of electrons for building biomass.

So this makes sense, but if it was so easy, why did water-splitting oxygenesis only evolve once? Oxygenesis therefore remains something of an unknown. It is possible that the evolution of oxygenesis was a Random Walk process, and consequently will be rare on other worlds. However, the biochemistry we have laid out above suggests that this is not so. Oxygenesis evolved fairly early in life's history on Earth, and there are good reasons for believing that it could evolve through a series of steps rather than requiring one huge leap of invention, many of which have evolved several times. If this is correct, then the ability to use water as a source of electrons and generate oxygen gas as a product is a Many Paths process, one which is likely to evolve on other worlds. And even if oxygenesis is a rare invention, this does not completely rule out the evolution of complex life, as we show in Chap. 9.

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6

Endosymbiosis and the First Eukaryotes

The prokaryotic world is composed of the domains Archaea and Bacteria (Box 1.1), which dominate our planet based on their sheer numbers. However, in the evolution of increasing complexity, the emergence of another major type of cell, the eukaryotic cell, was a critical innovation. While many eukaryotes are single-celled organisms, as are bacteria, some eukaryotes form multicellular lifeforms, in which cells form a larger organism that is much more than a collection of its parts (see Chap. 8 for more on multicellularity). Prokaryotes do not do this (although they can band together in simpler ways). Even single celled eukaryotes such as the protozoa can have extremely complex structures within a single cell, as exemplified by unicellular organisms such as *Paramecium* (Fig. 6.1). So how eukaryotes arose is central to our understanding of how complex life appeared on Earth.

6.1 What Is a Eukaryote?

Eukaryotic cells are structurally quite different from bacterial or archaeal cells. The eukaryotic cell keeps its DNA contained in an internal compartment, the nucleus, which is separated from the cytoplasm of the cell by a double layer of membrane, the nuclear envelope. The nuclear envelope has pores in it, complex constructions built from many proteins, to allow the nucleus to communicate with the rest of the cell. Other membrane-bound organelles exist as well, such as mitochondria and Golgi bodies (Box 6.1), and

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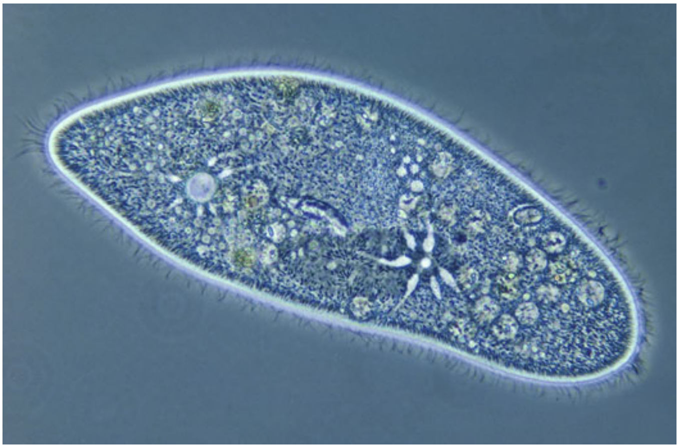


Fig. 6.1 Paramecium Caudatum, a complex predatory unicellular organism. Credit: M I WALKER/Getty Images

chloroplasts in green plants and algae. Eukaryotic cells are typically 10 times larger in linear dimension and about 1000 times larger in volume than prokaryotic cells. To manage all the internal structures of the cell the eukaryotic cell has an internal network of protein rods and cables called the cytoskeleton, that provides the cell with mechanical strength by including a system that functions like girders, ropes, and motors. Lacking the tough cell walls of most prokaryotes, eukaryotic cells from animals and protozoa (single-cell eukaryotic organisms) can change their shape rapidly and engulf other cells and small objects. This process is called phagocytosis and happens when a cell—for example, a protozoa or a white blood cell—engulfs a solid particle to form an internal vesicle known as a phagosome.

The genes that code for the eukaryotic cells are different from those of prokaryotes in three fundamental ways. The first is, of course, that they are segregated from the rest of the cell in the cell's nucleus, as we have noted. The second is that their control mechanisms are different and we will discuss this in Chap. 9. The third is that they are exchanged and shuffled by the process of sex, which we talk about in Chap. 7.

Box 6.1 The Eukaryotic Cell and Its Major Components

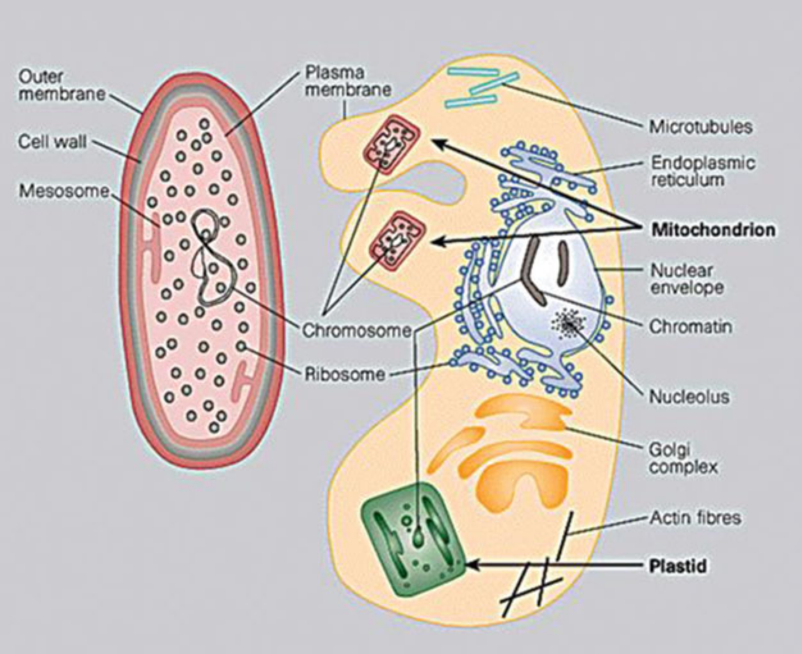
The internal complexity of a eukaryotic cell is critical for the development of complex life for three reasons. Firstly, the cell itself can be considered as an example of complex life. It contains more, diverse structures than a bacterial cell, and is itself an extraordinarily complex system, as a glance down a microscope at a *Paramecium* (Fig. 6.1) or an *Amoeba* will show. Secondly, the cell is more morphologically flexible, both literally and developmentally. Bacterial cells tend to have a single optimal size for their species—once the cell gets much larger, it divides into two. By contrast the internal structures of a eukaryotic cell allow it to be huge. The cytoskeleton can shuttle proteins or whole organelles around the cell, the localization of energy production and protein synthesis means that the cell can generate energy or make proteins a long way from the DNA. An extreme example of this is the vertebrate nerve cell, which can be a meter long, in the same animal that has stem cells that are only a few micrometers across. This opens the door to more complex life styles, and in a few groups of eukaryotes to multicellular lifestyles. Lastly, the large nucleus of eukaryotic cells enables more complex sophisticated genetic controls. We discuss the second and third points in subsequent chapters. Here we ask how that cell evolved, and whether that was a uniquely unlikely event.

The major components of a eukaryotic cell are:

- Nucleus—contains DNA (wrapped in a DNA:protein complex called chromatin), enzymes to make RNA from DNA, and machinery to control that process
- Ribosome—use RNA to direct the synthesis of proteins
- Cytoplasm—site of a lot of protein synthesis (on ribosomes), and many aspects of metabolism, including anaerobic generation of energy
- Endoplasmic Reticulum—organize ribosomes that are making proteins destined to end up in the membranes of the cell
- Golgi body—where proteins destined to be exported from the cell are processed and readied for export.
- Plasma membrane—external boundary of the cell, also contains proteins that signal to and from the outside medium to the inside of the cell.
- Mitochondrion—performs aerobic respiration (reacting food chemicals with oxygen to extract energy), as well as some other parts of metabolism, and coordinates cell survival under stress.
- Plastid—group of organelles containing pigments in plants, including chloroplasts which perform photosynthesis.
- Lysosome—membrane-bound body that breaks down unwanted or damaged cell components.
- Cytoskeleton—a general term for several types of microtubules and filaments of proteins such as actin in the cell that maintain and change its shape, enable it to move, and split the cell when it divides

(continued)

Box 6.1 (continued)



A eukaryotic cell (to the right) is much more complex than a prokaryotic cell (to the left). Major structural additions include the nucleus with the nuclear envelope and the cytoskeleton, which is made up of actin fibres and microtubules. Image from W. Ford Doolittle (*Nature).*

6.2 Origin of the Eukaryotic Cell

The origin of the eukaryotic cell was a key innovation on life's path to more complexity, especially since eukaryotic cells are so much more complex than prokaryotic cells, and all multicellular life is based on eukaryotic cells. Most scientists in the field agree that the genetic evidence suggests that the first eukaryotic cells must have evolved sometime between 1.6 and 2.1 billion years ago. The earlier limit comes from controversial claims of chemicals indicative of eukaryotes that were discovered in 2.1 billion years old fossils from West Africa. Microfossils found 1.6 billion years ago in North China show similar shapes and structures to eukaryotic cells. So eukaryotic cells are certainly ancient.

Most eukaryotic organisms have mitochondria, and those that don't contain other, chemically and structurally related organelles such as hydrogenosomes that are responsible for the energy production of those organism. Today mitochondria generate energy from oxidation of metabolites, and so would not have been expected to evolve before there was significant oxygen in the environment. The Great Oxygenation Event in Earth's history occurred about 2.4 billion years ago, when cyanobacteria produced so much oxygen that for the first time there was a marked rise of oxygen in our planet's atmosphere. The common view is therefore that eukaryotes arose with the appearance of mitochondria after the GEO. Thus the estimated origin of eukaryotic cells by about 2 billion years ago makes sense and is supported by recent paleontological research. We should note, however, that this is not a universal view. Notably, evolutionary biologists William Martin and Miklós Müller have suggested that the origins of the eukaryotic cell are more ancient, and derive from a collaboration between a hydrogen-making and a hydrogen-consuming organism in the anaerobic world before the GEO. As always, hypotheses about such distant events are hard to decide between. But all hypotheses accept that the eukaryotic cell did not arise on its own, but was the result of ever-closer collaboration between pre-existing organisms that came together in a process called endosymbiosis.

6.3 Endosymbiosis and the Origin of Eukaryotes

The first cell on Earth was almost certainly like a prokaryote, and did not have the complex internal structure of eukaryotic cells. So was the transition to eukaryotes uniquely improbable, or was it a Many Paths process? Luckily we have a good understanding to outline how eukaryotic cells came about (although many details remain to be discovered), and key to that process is endosymbiosis.

The role of symbiosis in the evolution of eukaryotes was championed in modern times by Lynn Margulis, who suggested it as a primary mechanism of evolution, and one that was instrumental to the appearance of the first eukaryotic cell.

Symbiosis is the close and often long-term interaction between two different biological species. Symbiosis is an interaction from which both species benefit, to distinguish it from parasitism in which the interaction is at the expense of one species. Traditionally, the term has been applied to organisms like lichens, which are not one organism but two that are totally mutually dependent, a symbiotic relationship between algae or cyanobacteria (or both) and a type of fungus. In the case of lichens, the symbiosis is obligate, meaning that the fungal and the photosynthetic symbiont cannot survive without the other. However, there are also examples of facultative or optional symbiosis, in which the two species can still separate and live on their own. A well-known example are cleaner fish that provide a service to other fish or even crocodiles by removing dead skin and parasites living on the skin of the host. This is an example of ectosymbiosis, when one organism lives on the other organism. However, an even more intimate relationship is possible, called endosymbiosis when one organism lives inside the other. Endosymbiosis is most relevant for us here, because it was involved in the origin of the first eukaryotic organisms.

6.4 Origin of Mitochondria

One of the more astonishing ideas of twentieth century biology is that mitochondria within eukaryotic cells originated from a free-living oxygen-metabolizing bacterium that was engulfed by another cell, and that chloroplasts in plants arose from the engulfment of photosynthetic bacteria. However, this has now been established beyond reasonable doubt, because both mitochondria and chloroplasts retained some of their original bacterial genetic code.

Mitochondria are organelles that are found in most eukaryotic cells (animal, fungal, protozoan), located in the cell's cytoplasm and surrounded by a double layer of membrane. With the help of oxygen, mitochondria oxidize the organic molecules, the cell's food, and produce most of the ATP to power the cell's activities. Mitochondria are similar in size to small bacteria, and like bacteria they have their own genome in the form of a circular DNA molecule, a genome that is not packaged up with histones like the eukaryotic genome is (we will talk about histones, proteins that package and order the DNA, more in Chap. 9). Mitochondria also have their own ribosomes to synthesize proteins. Bacterial and eukaryotic ribosomes are significantly different in shape and size and the proteins that make them up; and mitochondrial ribosomes are more similar to bacterial ribosomes than to those in the cytoplasm of eukaryotic cells (Box 6.1). Mitochondria also have own versions of other molecules necessary to make proteins, such as tRNAs and the enzymes that work with them. So by every criterion we can say mitochondria look like bacteria, except for two features; they live inside eukaryotic cells, and they have lost almost all of their genes. Modern mitochondria (and chloroplasts) have very small genomes, not nearly big enough to code for all the proteins they would need if they were to live as independent cells. Almost all the proteins in a mitochondrion, *including* the ones that look like they come from a bacterium, are actually made from genes in the nucleus and then imported to the mitochondrion.

This arrangement makes it nearly certain that mitochondria originated from free-living, oxygen metabolizing bacteria that were engulfed by an ancestral eukaryotic cell, and subsequently evolved to become part of that cell. That ancestral cell must have been anaerobic, living in an oxygen-poor environment, and otherwise unable to make use of oxygen. The bacterium that became the mitochondria might have escaped digestion, evolving in symbiosis with its engulfing host cell. It received shelter and nutrients in exchange for the power generation it performed for the host. Most recent research indicates that the aerobic bacterium that was engulfed evolved from a type of a purple photosynthetic bacterium (alpha-proteobacterium) that had previously lost its ability to perform photosynthesis and was left only with the metabolic ability for carrying out respiration. Given the diversity of mitochondria, it is possible that mitochondria originated from more than one endosymbiotic event. The genetic code used by mitochondria is usually slightly different from that used by the genes in the nucleus (and in bacteria today). For example, in the protozoan *Reclinomonas* the genetic code used by the mitochondrion is unchanged from the standard genetic code of the cell's nucleus, but in the mitochondria of mammals, fungi, and invertebrates the code is different—one of the 'words' in the genetic code has a different meaning in those mitochondria than it has in the genes in the cell's nucleus. These variations support the idea of different endosymbiosis events, but do not prove them as they could be the result of the dramatic events that causes mitochondria to lose nearly all their genes as they adapted to their new home.

There are some protozoa such as the intestinal parasite *Giardia* that do not have mitochondria at all even though they are eukaryotes. Does this tell us something fundamental about the origin of the eukaryotic cell? Scientists used to think that cells without mitochondria were descendents of an ancestoral eukaryote from before mitochondria appeared, and so mitochondria were not as basic and essential as people supposed. But this interpretation has been found to be false. All such eukaryotes contain organelles that are derived from mitochondria. Some contain hydrogenosomes, organelles involved in the anaerobic generation of energy from fermentation, which make hydrogen as a by-product, which are structurally and chemically similar to mitochondria even though they often lack their own DNA. Other organisms, such as *Giardia*, have gone even further and reduced their mitochondria to a remnant that plays no role in energy metabolism at all. However, they are still important for other cell functions, such as the assembly of proteins used elsewhere in the cell for energy metabolism. So it seems likely that all eukaryotes contain mitochondria or their descendents, that organisms which have no actual mitochondria have their reduced remnants, and that therefore mitochondria appeared in the earliest, original ancestor of all of today's eukaryotes.

6.5 Origin of Chloroplasts

Chloroplasts are another type of membrane-bound organelle found in photosynthetic eukaryotic cells such as those of plants and algae. Chloroplasts are the site of both the *Light* and *Dark* Reactions of photosynthesis, the process that takes the energy of sunlight and uses it to convert carbon dioxide into biomass. Chloroplasts, like mitochondria, have their own genome, characteristic 'bacterial-like' ribosomes and protein synthesis enzymes. Their genes show closest affinity to the cyanobacteria—bacteria which use chlorophyll in oxygenic photosynthesis—so chloroplasts almost certainly originated from cyanobacteria that were acquired by cells that already possessed mitochondria. The similarities between the genomes of chloroplasts and bacteria are striking with the basic regulatory sequences being virtually identical. The genomes of the chloroplasts of even distantly related plants such as tobacco and liverwort are near identical, and are closely related even to those of green algae. Once the cell incorporated a chloroplast there was no more need to chase after other cells as prey; the organism could settle down in a suitable location to take care of its energy needs. During subsequent evolution these cells have lost their ability to change shape rapidly and to engulf other cells, but developed a tough cell wall for protection. As with mitochondria, the chloroplast's DNA codes for only a small part of the chloroplast itself, the majority being coded by DNA in the nucleus and 'exported' to the chloroplast. Different chloroplasts have different pigments, which might suggest that chloroplasts were acquired several times independently; however molecular evidence opposes this idea, and suggests that chloroplasts were 'invented' only once. However even if this is so, the acquisition of chloroplasts and the acquisition of mitochondria were two separate endosymbiotic events, possibly separated by nearly a billion years.

The picture is complicated by the process of secondary endosymbiosis, where one organism that already has engulfed an organism can itself be engulfed by another. Consider the cryptophyte algae *Guillardia theta*, which went through several endosymbiotic events (at least three) and has four genomes: its own nuclear genome, the genome of its mitochondria, the genome of the chloroplast in its endosymbiont, and the genome of the endosymbiont's nucleomorph (nucleoid). Adrian Reyes-Prieto from Rutgers University claims that his process of serial cell capture and "enslavement" explains the diversity of photosynthetic eukaryotes.

6.6 Origin of the Nucleus

The eukaryotic nucleus is very different from how DNA is arranged in bacteria and archaea. We will discuss this in a lot more detail in Chap. 9, but here we just note that in terms of genetic machinery, eukaryotes are more closely related to archaea than to bacteria. One simple explanation for this is that eukaryotes resulted from the fusion of two or more cells, with the nucleus coming from an archaeal cell. Hyman Hartman and Alexei Fedorov conducted an in-depth study of eukaryotic signature proteins and concluded that the formation of the nucleus within a eukaryotic cell is best explained by invoking a hypothetical ancestoral cell they call a chronocyte, which engulfed a number of archaeal and bacterial cells. The nucleus would be the remains of the chronocyte. This kind of event would explain most similarities of eukaryotes to archaea, but also some commonalities to bacteria. A chronocyte is a type of cell that does not exist today, but is speculated to have had a cytoskeleton that enabled it to engulf prokaryotic cells and having a complex internal membrane system where lipids and proteins were synthesized. If such a cell existed, it must have had a complex internal signaling system involving ions, phosphates, and proteins. It would also explain how the planctomycete bacteria share some puzzling structural features with eukaryotes. Planctomycetes package their DNA into a membrane-bound compartment within the cell called the nucleoid. In all other respects their arrangement and control of their genes are typical of bacteria. But in this membrane the planctomycetes have a 'pore' structure to let material in and out of the nucleoid that is strikingly similar to the pores in the membrane around the eukaryotic nucleus, called nuclear pores, which have that function in our cells. If the chronocyte was to integrate its genetics with that of another cell, it would have to merge with a cell that could build nuclear pores. No such bacterial cells have been found.

Another proposal for the endosymbiotic origin of the nucleus was advanced by Philip Bell from Macquarie University in Sidney, Australia. He suggested that the eukaryotic nucleus evolved from a virus, likely a complex enveloped DNA virus similar to the present-day family of the Poxviridae or African swine fever viruses. His idea is that the virus established a persistent presence in the cytoplasm of a methanogenic archaea, and from there evolved into the eukaryotic nucleus by acquiring a set of genes that eventually usurped control of the host cell. Bell's hypothesis is supported by several eukaryotic features (such as messenger RNA capping and transport, the sexual cycle) that are difficult to explain with archaeal and bacterial genes only. Viruses are indeed known to be involved in many endosymbiotic relationships. However, the evidence that the nucleus originated from an endosymbiotic event, whether or not with the involvement of a virus, is still controversial within the scientific establishment.

6.7 Endosymbiosis Is a Common Phenomenon

Symbiosis is very common in the living world, including that most intimate of forms of symbiosis, endosymbiosis. There are two sorts of endosymbiosis, ones in which one organism holds another inside itself, and a second, even more intimate one where one organism enters into the cells of another. This second type is a direct analogy of what is believed to have happened at the origin of the eukaryotes, but we will review a few examples of the first type of endosymbiosis as well to show how widespread the general phenomenon is.

An important example of a symbiotic relationship is lichen, which as we mentioned above is a life form that consists of algae or cyanobacteria (or both) living among filaments of fungi. The close association between its biological components is so strong that a lichen has very different properties from any of its original organisms. Many different species of lichen exist in virtually every ecosystem on Earth. Many of the lichen species are the first colonizers of challenging environments such as deserts, rocky coasts, and high elevation alpine regions. In fact, lichens are so successful that it is estimated that up to

6% of Earth's land surface is covered by lichens. The fungus benefits from the symbiosis because the algae or cyanobacteria produce food by photosynthesis, while the algae or cyanobacteria are protected from the surrounding environment by the filaments of the fungus, which can often also provide enzymes and transport proteins to provide the photosynthetic organisms with the minerals that life needs. In most cases the filaments also help to anchor the organism. Although the association of photosynthetic organism and fungal cells is extremely close in lichens, the cells remain distinct.

The cyanobacteria or algae in lichens are not intracellular endosymbionts, as they live outside the fungal cells, and so are called ectosymbionts (although the photosynthesizing organisms are intimately mixed with fungi inside the lichen). However, this is not just one cell sticking to another. Ultramicroscopic examination of some cyanolichens (lichens where the symbiont is a cyanobacterium) show that the cell walls of both the fungal and the cyanobacterial cells are greatly thinned where they meet. While fungi have not taken cyanobacteria inside their cells as plants and algae have, they have nevertheless formed a close and intimate biochemical alliance with them.

We could cite many other examples of ectosymbiosis, but for our argument we are more interested in endosymbiosis, symbiosis where one organism lives inside the cells of another. This is very common, and widespread. Bacteria and fungi are found living inside the cells of corals, jellyfish, insects, fungi, and chordates—the group of animals than include vertebrates. There are even examples of bacterial symbionts living inside other bacteria, a direct analogy of what is believed to have happened at the origin of the eukaryotic cells. Thus, you do not have to be a eukaryote to have an endosymbiont.

In corals, photosynthetic dinoflagellates live inside the cells of the coral animals. The genus *Symbiodinium*, also known as *Zooxanthellae*, provide energy through photosynthesis, in return for protection and other nutrients. The ciliate *Paramecium bursaria* also hosts unicellular green algae within its cell. While *Paramecium* benefits from the food synthesized by the alga, the alga benefits from the host's ability to transport it to a location where there is light. *Paramecium* can be cultured apart from the alga, but then must be supplied with extra food to survive.

Endosymbiosis is extremely common in insects, especially in those that depend on nutritionally restrictive diets such as woody material, plant sap, or vertebrate blood. It has been estimated that about half or more of the 1.2 million insect species harbour endosymbiotic bacteria, mostly *Proteobacteria*, *Actinobacteria*, *Clamydiae* and *Firmicutes*, living inside the cells of their guts. In many insect species the endosymbiosis is obligate—host and bacteria cannot survive apart from each other anymore. An intriguing example of this close association is observed in the pea aphid *Acyrthosiphon pisum*, which sucks juices from its host plant. The plant sap lacks certain amino acids, which the aphid cannot make. However, an endosymbiotic gamma proteobacterium called *Buchnera aphidicola* that lives inside specialialised cells inside the aphid can make those amino acids, and provide them for the aphid in return for other nutrients, protection and mobility. The aphid also makes some of the enzymes that the bacterium needs to make its cell wall. The aphid cannot survive without specialized cells within its body that contain the bacterium, and the bacterium cannot live outside the aphid. The aphids have even evolved a specific mechanism to transfer bacteria from mother to offspring. They are maternally inherited by an elaborate mechanism, in which the symbiont directly infects the embryos within the maternal body.

Not all endosymbiotic associations in insects are so close, and there are many examples of endosymbiosis where the host can live without the symbiont. In these cases the symbiotic bacteria are usually not bound to one specific location, but are found within a range of host tissues, even outside of the insect. Examples for these facultative associations are bacteria that endow their insect host with tolerance to high temperatures, fungal pathogens, and increased resistance to parasitoid wasps. In the scientific literature facultative endosymbiosis has often been associated with parasitic strategies, in which the parasites sometimes evolve to provide some benefit to the host.

However, even in parasites themselves we observe endosymbiosis. A quite bizarre example with a very close association must have occurred in the protozoan parasite *Toxoplasma gondii*. The pathway for abscisic acid production in the parasite, which infects about one-third of the world's human population, appears to be derived from a relict endosymbiont, acquired by the ingestion of a red algal cell. Thus, this type of mutualism is even more extreme, with transfer of not only the genes from the endosymbiont to the host, but also some of the functions like the signalling pathway (though the photosynthetic capability of the endosymbiont has been lost). The presence of an apicoplast, a non-photosynthetic chloroplast-like organelle found in most protozoan parasites, including malaria parasites such as *Plasmodium falciparum*, is another intriguing example. These plasts derive from a secondary endosymbiosis of the protozoa with a type of alga.

It is not only bacteria that are endosymbionts. Christina Preston from the University of California—Santa Barbara reported that a marine archaeal species of Crenarchaeota, a phylum that is often associated with sulphur metabolism and tolerance to high temperatures in the marine environment, inhabits the tissues of a temperate water sponge. This association is so specific that only a single crenarchaeal species inhabits a specific sponge host species.

This was the first endosymbiosis reported for any species of Crenarchaeota. Interestingly, the archaeal symbiont grows well at temperatures of 10 °C, over 60 °C below the growth temperature optimum of any cultivated species of Crenarchaeota.

Another no less astonishing example is the reported unique ability of a bacterium to enter the mitochondria of the tick *Ixodes ricinus*. The intracellular bacterium, apparently an alpha proteobacterium, was found to be localized both in the cytoplasm and within the intermembrane space of the mitochondria of ovarian cells, and was the first bacterium found to reside within animal mitochondria. The group of scientists led by Davide Sassera from the University of Milan in Italy and Nathan Lo from the University of Sydney in Australia suggested the bacterium be named "*Candidatus* Midichloria mitochondrii", a link to the fictional midi-chlorians in the Star Wars universe where they are thought of as intelligent microscopic life forms that live symbiotically inside the cells of all living things.

Most well-studies endosymbioses are between animals or protozoa and other species, but endosymbiosies between fungi and other species are well-known as well. One of the most important examples are mycorrhiza, the symbiosis of fungi living in the roots of plants. The fungi benefit by that relationship from having shelter, while the plant, in turn, benefits from the inorganic nitrogen and phosphorus absorbed from the soil by the fungi. This symbiosis was very important for the colonization of barren land surfaces in the Silurian, from 443 to 416 million years ago, as the kind of mutualism that allowed plants to colonize land surfaces on which plants alone would otherwise not have been able to grow. Some fungi colonize plant roots on the outside, but others enter the plant root cells to become endosymbionts. Eighty percent of land plant families today have endosymbiotic mycorrhiza.

Usually endosymbionts are recognizable as whole organisms, even if they are no longer able to survive outside the host cell. But some examples are known where the endosymbiont has lost genes or cell structures—in a few cases more than 70% of its original gene content—to become in effect a 'missing link' between a symbiotic organism and something like an organelle. An example is the flagellate unicellular organism *Hatena arenicola's* "eyespot" (photosensor), which it inherits from a symbiont that belongs to the genus *Nephroselmis* (a green algae). The symbiont retains its nucleus, mitochondria, plastid, and occasionally a Golgi body, but the flagella, cytoskeleton, and endomembrane system are lost. In this remarkable host-symbiont partnership the symbiont is always inherited by only one of the daughter cells. The one that does not inherit the eyespot is colorless instead of green and develops a feeding apparatus in the location of the eyespot in the symbiont-bearing cells. The colorless

Hatena is able to prey on other cells and engulfs free-living cells of *Nephroselmis*, a genus quite common in its habitat. Next, the feeding apparatus degenerates and the symbiont plastid develops. Since the scientists never observed any dividing cell without the symbiont, the symbiont acquisition and modification must occur within one generation. The presence or absence of the symbiont alters the morphology and physiology of the host cell. The process is strain-specific. When Noriko Okamoto and Isao Inouye used a different strain of the same species the symbiont was engulfed and remained undigested, but did not undergo the modification to become an "eyespot". The example of the *Hatena* is likely an early stage of endosymbiosis, until a solution by the organism can be found to transmit the symbiont eyespot to both daughter cells.

Modern DNA sequencing has been done on some of these bacterial endosymbionts. Some retain a full set of genes, like a free-living bacterium. But many others have lost genes, in some cases most of the genes in the cell, and are completely reliant on their host for many biochemical processes. An example is the endosymbiont bacterium *Carsonella* ruddii, found in many sap-feeding aphids. It has only 140,000 bases of DNA in its whole genome. This may sound like a lot, but the genome of *Mycoplasma genitalium*, a highly 'stripped down' parasite that cannot live outside mammalian cells, has 420,000 bases, and most free-living bacteria have genomes of over a million bases. Such genome reduction has an obvious analogy with how genes were lost from the bacteria that ended up as chloroplasts and mitochondria in modern eukaryotic cells.

We mentioned bacterial endosymbionts inside bacteria. These are hard to detect. Most methods of finding bacteria in samples do not look inside the bacterial cells; they analyse their genes, and a bacterium inside another bacterium just 'looks like' two bacteria. However, the endosymbiotic bacteria in the Mealybug have been found to have endosymbiotic bacteria inside them—a bacterium inside a bacterium. Less beneficial are the relationship of an entire class of bacteria called Bdellovibrios, which live inside bacteria as parasites. They have a partially symbiotic, partially parasitic relationship with their host cells, taking more than they give but not killing the host. One Bdellovibriobacterium has been found inside a cyanobacterium that is itself an endosymbiont of marine sponges.

There are hundreds of other examples of endosymbiosis. Our illustrative examples show that this mode of life is widespread, must have evolved many times, and includes direct analogues of what is believed to be the earliest precursor of the eukaryotic cell—a bacterium living symbiotically inside another bacterium.

6.8 The Next Step

Recurrent endosymbiosis events resulting in mitochondria or an equivalent organelle, and possibly also the origin of the nucleus as a result of endosymbiosis was a critical novelty for the eukaryotic organisms providing it more power and a selective advantage because they could now grow bigger, more complex, and consume other organisms. However, becoming larger meant a smaller surface area to volume ratio associated with a lower rate at which material can be moved through the cell and nutrients can be taken up, thus a selective disadvantage for any pre-eukaryotic cell competing for limited resources. Perhaps this helps explain why it took so long for eukaryotes to evolve. The fitness hurdle had to be overcome. Only a more advanced version of a eukaryote with mitochondria would be able to compete with the prokaryotic world. Or, the rise of eukaryotic-like organisms was simply not possible earlier due to the lack of oxygen in the environment. The fact for life on Earth remains that prokaryotic organisms arose about 3.8–4.2 billion years ago, while eukaryotic organisms seem to have originated about 2 billion years later.

Of course, saying that endosymbiosis is common is not the same as saying that the origin of mitochondria and chloroplasts was an easy evolutionary step. There had to be dramatic changes to the physiology of symbiont and host, including gene transfer from the symbiont to the host nucleus and the establishment of a molecular machinery for protein transport back into the symbiont. Furthermore, it requires the synchronization of the host-symbiont cell cycles and the transmission of two or more linked genes on a chromosome to the same daughter cell leading to the inheritance of these genes by the offspring. How that synchronization did occur is not known yet and a field of further research. For both mitochondria and chloroplasts, many metabolites have to shuttle between the organelle and the cytoplasm, including ATP. How this is achieved is well known, but how it evolved is more of a mystery.

However, it might be that endosymbiosis is not the only route to the evolution of greater complexity. The type of internal compartmentalization we see in eukaryotes as a result of endosymbiosis we also observe in some prokaryotes, although the internal structure in eukaryotes is much more complex and extensive. The phylum *Planctomycetes* of the domain Bacteria has a cellular structure in which the cell cytoplasm is divided into compartments, including a major cell compartment containing the nucleoid. Of special importance in this regard is the species *Gemmata obscuriglobus*, in which the nucleoid is enveloped in two membranes to form a nuclear body that is analogous to the structure of a eukaryotic nucleus. In addition, many

Planctomycetes have also an intracellular membrane-bound compartment for carrying out anaerobic ammonium oxidation reactions. Some archaea also have internal membrane compartments. Thus, assertions that intracellular membranes are unique to the eukaryotes are incorrect. The intracellular membrane system of eukaryotes is integrated into a dynamic network of vesicle trafficking and control that appears to have no equivalent in bacteria and archaea. However, some of the core proteins and structural elements of the cytoskeleton are also found in prokaryotes, suggesting that the eukaryotic cell architecture is an elaboration of a system that was either pre-existing in the common ancestor or has evolved several times since. The compartmentalization in the prokaryotes may indicate that there may be another option for the origin of the eukaryotic cell structure and if so, we cannot completely exclude the possibility that the first eukaryote on Earth evolved from a *G. obscuriglobus*-type organism. On the other hand, the double-membrane of *G. obscuriglobus* could simply be evidence that its nucleoid originated from endosymbiosis.

Eukaryotes might have evolved as predators with a size advantage that allowed them to capture and consume other organisms. The cytoskeleton also supports the idea that the first eukaryote was a predator; and the invention of the nucleus could possibly be attributed to this life style—protecting the DNA from damage by movement of the cytoskeleton. The cytoskeleton is a critical asset for the eukaryotic cell. In a smaller prokaryotic cell nutrients can be obtained by diffusion, however, a larger cell has to move organelles as large as a ribosome or a mitochondrion around. This is achieved by a dynamic network of vesicle movement and control, and complex internal structures that rival in their complexity small multicellular organisms. The mitochondria with their enormous involuted internal membrane structure provide the power, and the cytoskeleton allows the execution. However, some of the core proteins and structural elements of a cytoskeleton are also found in prokaryotes. For example, the giant bacterium *Epulopiscium fishelsoni* has an internal tubule system so similar to eukaryotes that it was initially mistaken for a protozoan.

6.9 Eukaryotic Organisms on Other Worlds?

While many paths may have been taken in the evolution of the complex cell structure of eukaryotes on Earth, they clearly took a long time. The fact that life existed for nearly 2 billion years before we find evidence that the eukaryotic cell emerged is empirical evidence that this is so. *Many Path* processes are likely to occur within a defined time 'window', with the timescale depending on the pace of the underlying individual component innovations, and the width of the ‘window’ depending on the number of possible innovations and the number of actual innovations needed to achieve the overall function. This would also be the case on other planetary bodies on which a substantial biosphere arose. As the timing of the appearance of eukaryotes on Earth is uncertain, it will be hard to constrain either the timescale or window. However, the analysis does not depend on doing so, and does suggest that evolution of a complex cell comparable to those found in plants, animals and fungi will also occur on some other planet or moon with a sufficiently large and diverse biosphere.

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7

Sex: A New Way of Reproduction

People think sex is important. They may be right.

When biologists talk about sexual reproduction, they are not talking about all the fun, intimate stuff that teenagers fear that their parents are still doing. That is quite incidental. Sexual reproduction is how two individuals take their genes, shuffle them, and produce a new individual. Almost all eukaryotes can reproduce sexually, where the chromosomes are doubled up and then a complex mechanism ensures that each daughter cell gets exactly one copy of the complete set of genes. It is a fearsomely complex process, and one fraught with risks for both the parents. And yet every eukaryote (with a few interesting exceptions we will mention later) seems to do it. Why? And is this one of the critical steps on the way to complex life?

7.1 The Geography of Genes

To understand sex, we need to take a step back, and understand how genes are arranged in eukaryotic cells. Our genes are segments of DNA. The DNA in an organism can be a few hundred thousand bases in the simplest of bacteria to around three billion in humans, more in some other species. A DNA molecule three billion bases long would stretch 45 centimeter if it were a rigid rod, which obviously cannot fit into a cell a few micrometers across. So the DNA is folded into tight bobbins around proteins, and the bobbins are stacked into larger structures, so the DNA can fit inside a single cell. This is common to all life.

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In eukaryotes the proteins are called histones and the bobbins have a very specific and uniform structure. They are stacked up into further structures which, as we will discuss in Chap. 9, are the key to how the genes work. However we are concerned here with how the genes are inherited, and that is made more complicated by that fact that those three billion bases of DNA are not in one molecule in humans but in 23 molecules, called chromosomes. They are linear, and have distinctive middles and ends. All eukaryotes have this arrangement, although the number of chromosomes varies from just one in males of the Jack Jumper ant to 134 in the arctic-dwelling Agrodiaetus butterflies.

The ends are actually a problem, as the enzymes that copy DNA cannot copy the ends of molecules. So if there was not a special 'fix' for the ends, each time we made a copy of a chromosome we would lose a bit off the end. After a few duplications the chromosome would start to lose essential genes, and that would be fatal. So eukaryotes have evolved specific structures at the end of the chromosomes called telomeres, and a specific set of enzymes to replace them. Interestingly, in multicellular organisms such as ourselves this mechanism is not perfect, and there may be a reason for that which we will touch on in Chap. 8.

Bacteria generally have a simpler solution. Their chromosomes usually have no end. Their DNA is a circle. So the DNA-copying enzyme can start at a specific site, and run round the molecule all the way back to the start without ever coming to an end (however, some bacteria have linear chromosomes, so the linear chromosome aspect of our genetics is not unique).

There are two issues with the genetic arrangements of eukaryotes that arise from cell division. When a cell divides into two, both cells need a copy of all the original cell's genes. If you have just one, long molecule of DNA, then you have to make sure that each cell gets a copy. But if you have (as in humans) 23 molecules, you need to make sure that they are all duplicated and then one copy of each ends up in each of the two daughter cells correctly. Eukaryotic cells have a complex set of molecular machines in the cell to make this happen.

This means that the cell starts out with a set of chromosomes, duplicates them so it now has twice the number, and then equally partitions them into a pair of new cells. Bacteria do the same, of course, but usually with only one chromosome, and with a correspondingly less complex apparatus.

Eukaryotes have evolved a much more sophisticated system, called sexual reproduction. They take two cells with one set of chromosomes each, which are called haploid cells. They fuse them together, so you now have a cell with *two* copies of all the chromosomes; this is called a diploid cell. That diploid cell then undergoes two rounds of division, ending up with four cells. During the first the chromosomes pair up and swap segments, making a new set of pairs of chromosomes, two of each. There is a complex set of enzymes specifically to do this, and evolution of these was a key step in the development of sex. The cell then divides again, but without duplicating the chromosomes, so you end up with four daughter cells each with one set of chromosomes, but with a set of genes derived from two parents. The process of taking a diploid cell, swapping segments of its chromosomes, and then splitting them to form haploid cells again is called meiosis. This haploid/diploid cycle is something that almost all eukaryotes can do.

7.2 The Alternation of Generations

We have implied that the 'normal' cell is the haploid cell, and that the diploid cell is a brief interlude in its life. For some forms of life—quite a few fungi, many protists, mosses, this is true. But there is no reason why the diploid cell could not live as an individual organism in its own right. It has all the genes it needs—two copies in fact—so it could duplicate the pairs of chromosomes and then send *two* copies of each chromosome to each daughter cell. So which happens—is the haploid cell the 'normal' form or the diploid?

It depends on the organism, but in most complex organisms the diploid form is the dominant one. We cheated here, when describing human cells. Human cells have 23 *pairs* of chromosomes—human cells are diploid. When they divide, the cells double the pairs up, then send one set of pairs to each daughter cell during cell division. We do make haploid cells, but they are small, specialized and not able to live on their own. They are the sperm and egg cells, together called gametes, that we spend so much time on social media sites and at parties trying to get together to form a new diploid cell. Land plants similarly are diploid, and their haploid parts are the pollen and 'egg' that fuse to form a new plant without ever leading an independent existence. However, mosses are haploid. They make haploid cells that fuse to form a tiny diploid organism called a sporophyte, which can then swim to a new location, split into haploid cells again and start a new plant. Seaweeds and most fungi are haploid.

Most organisms use special cells for reproduction, and from very early in their development they set aside a set of cells that will become the reproductive cells of the adult animal or plant. The famous German zoologist August Weismann called this the separation of the Germ Line and the Soma: Germ cells are the cells that will go on to make haploid cells, and hence the next generation, and the Soma is everything else. Richard Dawkins famously commented that the reason for the Soma's existence was to allow the germ cells, and the genes in them, to breed; we, the diploid soma, exist solely so our germ cells and the genes they carry can get together and make the next generation. But while Germ Line and Soma are strictly separate in higher animals, they are not in most other complex organisms, even in complex plants, which can be grown from cuttings or root fragments to make plants complete with flowers that can set seed.

7.3 So Why Have Sex?

Sex evolved quite early in the history of the eukaryotes, possibly at the same time as the eukaryotes themselves. It only evolved once, but there is still debate among evolutionary biologists about *why* eukaryotes bother with sex. The risk is substantial. You have to find another cell to fuse with. You have to share your whole genome with that cell. What if it contains parasites? And then you end up with daughter cells that only have half your genes. If you just went and split in two, both the daughter cells would have all your genes—on a *per gene* basis, that is a clear winner. There are a number of arguments about what use sex is, but scientists have not reached a consensus about which is right.

7.4 Speeding up Evolution

Imagine that you only had one parent, that parent had had one parent and so on back to the time of the dinosaurs. This is clonal reproduction—you would be genetically identical to your parents in the absence of any mutations, they would be identical to their parents and so on. As the environment changed, the species needs to change its genes to suit the new environment. This could be by accumulating beneficial mutations, but that is slow. Also, most mutations are actually bad for the organism concerned, and so there is a balance between wanting mutations and avoiding them.

Microbial forms of life have evolved a way around this, in that they swap DNA. If one bacterium has a set of genes that (for example) makes it resistant to antibiotics, and another has a set that (for example) makes it invisible to our immune system, then if they exchange them the new bacteria are the perfect 'superbug' infectious agent, and can colonise a new environment—people. Bacteria can do it through a wide variety of ways and in DNA of all sizes. Bacterial genomes are a patchwork of segments that have been transferred from other organisms in their evolutionary past. This is Horizontal Gene Transfer

(Box 4.4). But that is unstructured and risky, and also only benefits the recipient of the DNA.

Historically it has been argued that sex is a better mechanism for this gene exchange, allowing faster adaptation to new environments by complex organisms. It allows a life form to gather the best mutations together in one cell by re-arrangement of the chromosomes and exchange of genetic material. It also allows for there to be two copies of a gene in one cell. One of these can be changed, and not leave the cell without that genetic function, as the other copy is there to take up the load. This might be the first step in gene duplication that we mentioned in Chap. 5. More recently this view has been challenged, and sex is seen as a way to provide the flexibility of the haploid cell when times are good with the DNA-backup of the two copies of each chromosome in the diploid cell when times are bad, and in particular when you are being dried out in the sun and exposed to UV irradiation. It has also been suggested that sex provides the genetic variation you need for the slow-mutating nuclear genes to keep up with the faster-mutating genes in mitochondria. Sex does also create new gene combinations, which allows faster adaptation to new environments.

The problem with this argument is twofold. The first is that it is not clear that the benefits of adaptation are high enough to offset the costs of sex. But the second, even worse, is that this is a long-term argument, and evolution does not have any foresight. It acts only on this generation, there is no ‘guiding hand’ to plan for the future. And the evolutionary argument is about the future, not about today.

7.5 Avoiding Mutations

A related idea is that sex evolved to avoid the damaging effect of mutations without avoiding the mutations themselves. You do not want to avoid all mutations, as that would stop evolution completely, and your species would ultimately become extinct. (Anyway, avoiding *all* mutations is chemically impossible. The molecule of DNA cannot be protected against all damage in a cell full of activity and chemistry.) But most mutations are deleterious. So sex is a way of taking a copy of a chromosome that may have a mutation on, a copy that does not, and shuffling them. The process of shuffling (called Recombination) can correct some DNA damage, fill in missing bits of genes, as well as swap segments of genes around. The result is a genome in which mutations are both repaired and shuffled between individuals.

The problem with this as an explanation is that, again, bacteria have the same enzymatic mechanisms for repairing mutations. Some do it far more efficiently than eukaryotes; the bacterium *Deinococcus radiodurans* can withstand a dose of radiation that would completely destroy the genome of a eukaryote, because its repair mechanisms are much more efficient (it is so tough it has been nick-named "Conan, the Bacterium"). Sex is not the only way to keep mutations in check.

7.6 Avoiding Parasites

Another view is that sex is not there to evolve good things, but to avoid bad ones. The argument suggests that the bigger and more complex you are and the more energy you accumulate in healthy tissue, the more you are a target of parasites. If an organism reproduces as a clone and its offspring is genetically identical to itself, then any parasites that can attack the parent can attack their children. If a parasite evolves that is perfectly adapted to attack the parent, it will wipe out the whole family, indeed the whole species. However, if offspring are subtly different from the parents and from each other, parasites will only be able to attack a few of them, and the family will pass its genes on to the next generation. Whole classes of genes in mammals are dedicated to making our cells look different from each other (a side-effect of this is that you cannot exchange blood or tissue between people easily; they have to be 'matched'). Those genes are swapped by sexual reproduction, making it harder for parasites, from viruses through bacteria and protozoa to insects, to attack us. Constantly shuffling those genes makes us more resistant to parasites.

The problem with this argument is that bacteria have evolved mechanisms to do this without sex. They can swap genes (as noted above) and have internal mechanisms to defend against viruses. The recently discovered CRISPR system is a widespread mechanism that takes pieces of invading viruses, stitches them into the bacteria's own DNA, and then uses that new piece of genetic information to identify that virus in the future and destroy it as soon as it enters the bacterial cell. It acts like our immune system, but better than our immunity it is inherited from one bacterium to the next. Other mechanisms exist—the malaria parasite (a eukaryote) can shuffle its genes internally to change its surface chemistry and so evade our immune system. It does not need sex to do this. So there are lots of other ways that have evolved to avoid parasitism. Why sex?

There are many other theories such as that sex is there to clean up mutations that accumulate in mitochondria (mitochondrial DNA mutates faster than the DNA in our nucleus).

So sex might be useful sometimes, but life has evolved other ways to do everything that sex does. The odd thing is that almost all multicellular organisms *must* reproduce sexually. Plants can be propagated asexually (through cuttings), and some spread without sexual reproduction. Many grasses, strawberries, sumac trees, all spread by sending out roots or runners and making new, identical plants. But it is an observation that plants which grow as clones—a group of organisms that are genetically identical because they reproduce without sex—eventually die out. Some animals such as aphids can reproduce asexually, but they only do so for some time of the year, resorting to sex when autumn comes. Boa constrictors have recently been seen to reproduce without fathers (mother-only reproduction, called parthenogenesis), although the genetic mechanisms behind this may still involve the cellular mechanics of sex (i.e., the chromosome shuffling), just within the mother. Whether they can do it for many generations is not known, but the precedent suggests that Boas will use sex most of the time, resorting to parthenogenesis only as a last resort when males are rare. In fact, it seems an almost cast-iron law that complex life needs sex, and avoids it only as a last resort and for a few generations at most. Does this mean that the evolution of the complex apparatus of chromosome pairing, exchanging and separating has to evolve before complex organisms can evolve, and if so, is this a Random Walk event?

We think sex is not as unique and limiting, for three reasons:

7.7 Celibate Complexity

Firstly, there *are* multicellular eukaryotic organisms that do without sex. They are rare, so rare that evolutionary biologist John Maynard-Smith has called them “an evolutionary scandal”. But they show that complexity itself does not require sex.

The most well-known example are the Bdelloid rotifers, microscopic predators that live in fresh water all over the world, from ponds and rivers to the film of water around particles of soil. The Bdelloid rotifers have genomes that are completely incompatible with the pairing-and-separation dance of meiosis, and show that they have evolved without sex for at least 10 million years. They are genuine multicellular organisms, with a complex anatomy and behaviour. How do they avoid the problems that sex is meant to solve?

One reason proposed for sex is that it speeds up evolutionary innovation. This might not be such a problem for rotifers, as they are astonishingly numerous: a cubic meter of pond water can contain more rotifers than the human population of Beijing or Karachi. With such a huge population to work on, it is argued that rotifers do not need the extra evolutionary boost that sex might give them.

This is an extension of a common observation about plants that propagate asexually. They tend to be small, weedy plants that rapidly colonize new environments, like dandelions or turf grass. They have genomes ideally suited to their new environment, and so do not benefit from the evolutionary boost given by sex. And their lifestyles require fast growth, not waiting to have seed fertilized before the next generation can start out. But unlike Bdelloid rotifers, they do need sex every dozen or hundred generations to avoid dying out.

Another reason proposed for sex it to overcome mutational damage, and acquire new traits. The Bdelloid rotifers side-step this need with an extraordinary strategy. They seem to be able to acquire new DNA like bacteria, in smaller segments acquired from quite different organisms. Their genomes are a patchwork of DNA apparently from different individual rotifers, and some from other organisms, even bacteria. How they acquire this foreign DNA is still a mystery, but clearly it is not by having sex.

Bdelloid rotifers are not the only organisms to do without sex. Ostracods are tiny crustaceans (the same family as shrimp and lobsters) that live in fresh waters around the world. Darwinulid ostracods originated in the Carboniferous Period 359–299 million years ago (Box 1.2), and some may have done without sex ever since. They have an unusually adaptable set of genes, which perhaps means they can tolerate more genetic damage than most animals. They also carry out gene conversion, the process by which one gene is used to ‘correct’ the sequence of another, at an unusually high rate. This is a process like the gene-swapping recombination that occurs in meiosis, but it happens between the chromosomes in a normal diploid cell. In principle, this could allow the ostracods to correct mutations more efficiently.

Orbatid mites are yet another group, originating in the Silurian Period, 443–416 million years ago. They are tiny soil-dwelling animals, again common in many parts of the world. They can evolve—since the Silurian they have evolved into about 10,000 distinct species, all apparently without sex. They do, however, retain the apparatus of meiosis.

Many simpler plants and some fungi also seem to be able to reproduce indefinitely without sex. So we can learn two things from this. Firstly, it is possible for complex, multicellular animals to evolve that can do without sex, and also for a range of simpler organisms. Secondly, for each of the proposed reasons for sex, other approaches seem to work for those organisms.

The third point is indirect, but we think it is important. The mechanics of meiosis are central to sexual reproduction, and yet they vary quite a lot between species. For example, the proteins and DNA sequences that link the chromosomes to the cytoskeleton to winch the new chromosomes into the daughter cells on division have evolved rapidly (in evolutionary terms), suggesting that the specifics of how they work can relatively easily be changed.

So we interpret sex not as a key innovation, but a particular mechanism to ensure regular genetic exchange between parents to create new offspring, one which is just one of several possible such mechanisms and hence the outcome of a Many Paths process.

7.8 Dating

We cannot leave sex without touching on all the anatomy and behaviour that complex life-forms develop in order to get one gamete to fuse with another and make a new individual. Flowers display colours and scents, and in animals a wide range of anatomical structures and behaviours are used to attract a suitable mate. Larger mammals seem to spend quite a bit of their time doing nothing else. Once the basic apparatus of the haploid/diploid cycle has been built, organisms have found an astonishing variety of ways to get two cells together. The evolution of this aspect how sex is done is definitely a Many Paths process.

Sexual reproduction is not as rigidly defined as a mammalian observer might think. The fungi show an enormous range of sexual reproductive arrangements, with species showing between 1 and 12 mating types (“genders”), and (importantly) strong evidence of rapid evolution between different mating type arrangements and, in some species, the ability to switch between reproductive strategies. In mammals your sex is determined by a pair of chromosomes called X and Y, the only two of the 23 pairs of chromosomes that humans have that are not exact copies of each other. If you are XX, then you are anatomically a female, XY is anatomically a male. But in birds it is the opposite—the chromosomes are called Z and W rather than X and Y, but the ZW arrangement is female and the ZZ is male. Some reptiles have the XY system of mammals, but which sex they grow up as depends on the temperature. All of this suggests that, once a complex system of genetic exchange has evolved, all the mechanisms for making it work, for selecting a mate, and for producing new offspring have evolved many times and this is also a Many Paths process.

7.9 Big Is Sexy?

We cannot quite leave it there. All the examples of asexual animals are small, common organisms. All the examples of asexual plants and fungi are fairly simple. Could it be that sex—not just genetic exchange but the complex dance of the chromosomes that is meiosis—is needed to develop large, sophisticated animals? There is a vast population of Bdelloid rotifers on Earth, thus a relatively inefficient genetic correction system might be overcome by sheer numbers. The same logic cannot apply to elephants or giant redwood or even to people, which are a rare species compared to rotifers or soil mites. Until we have a complete and agreed understanding of why sex evolved, and why almost all animals and most plants seem to depend on it, we cannot say. Until then, we favour the argument that the specific mechanisms of sex—the dance of the chromosomes, the dance of the dating game—evolved only once, but the functions of finding a partner to exchange genetic material with and carrying out that exchange is a Many Paths process.

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8

The First Multicellular Organisms

8.1 Multicellularity: A New Strategy for Life

All life is made up of cells. Unicellular organisms, as the name suggests, have just one cell, although that cell can be enormously complex. Multicellular organisms contain not just many cells, but critically they contain cells that are different from each other. Originating from a single egg, they develop into different cell types that have different functions. It is this specialization that allows multicellular organisms to develop complex structures such as leaves, eyes and brains. Hence the definition of a multicellular organism put forward by G. Bell and A. Mooers in 1997, that multicellular organisms are clones of cells that express different phenotypes despite having the same genotype. The 'phenotype' is the physical characteristics of a cell or an organism that the genes program. For example, in humans, liver and brain and muscle cells all have the same set of genes and all derive from one fertilised egg cell, but they are clearly extremely different. This definition captures the most distinctive property of multicellular organisms. Differentiation and eventually specialization within a group of cells with the same genome leads to the increased complexity that we attribute to multicellular organisms. While all the cells of an individual organism have the same genomes, different sets of those genes are active in different cells within the organism. The only clarification which we might want to add to the pointedly short definition by Bell and Mooers is that this achieved differentiation has to be of a cooperative rather than a competitive nature.

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To make this collection of cells work, they must work together, and that means three things. It means cells must communicate and stick together. Even in the nematode worm, *Caenorhabditis elegans*, as many as 2000 genes encode for cell adhesion and cell signalling. It also means that the cells must activate their genes at different times and places, which means complicated control systems for the genes, called 'genetic control circuits'. The more complex the organism, the more complex these circuits are. For example, the group of proteins called "helix-loop-helix family", one of many families of proteins that regulate how genes work in all eukaryotes, has 41 members in *C. elegans*, 84 in the fruit fly *Drosophila*, and 131 in humans, while there are only 7 of those in unicellular yeast, reflecting the relative complexity of those organisms. And lastly, the cells must be willing to cooperate, sacrificing the ability to do some things in order to specialize in their principle function. The social collaboration within a multicellular organism is so close and intricate that it even extends to the self-sacrifice of the somatic cell for the sake of the germ cell and the perpetuation of the species. This is very different from unicellular organisms where the principle rule is the survival of the fittest, or perhaps more accurately the survival of the "fit enough". In a multicellular organism, this is still the guiding principle for the whole organism, but not for the somatic cell. Ultimately all somatic cells are destined to die. The reason behind that strategy is that all cells within a multicellular organism are clones of each other, thus the germ cells perpetuate the genome of the somatic cells as well as their own to the next generation—a successful strategy indeed if judged by the success of multicellular organisms on Earth.

Of course, the system is not perfect, and very rarely a cell in a multicellular organism mutates and loses its social control. It starts to divide without regard for the needs of the organism around it. That is a problem for a multicellular organism as large, and hence with as many cells, as a mouse or a human. An adult human is made up of something like 40 trillion cells, most of which are replaced on a timescale of months as they wear out or get damaged. So over a lifetime, a human might have to grow 20,000 trillion cells. Every one of those cells must behave according to the overall program. In a bacterial colony, if one bacterium can grow faster than the others then that bacterium's offspring will eventually dominate the colony. That cannot be allowed to happen in a multicellular organism; if one cell gains a mutation that makes it grow faster, or where it is not meant to, the result is a cancer that will kill the organism. How does a multicellular organism therefore keep control of every one of those trillions of cells?

The answer is that it needs yet more controls on what the cells do, including some fail-safes. There are several mechanisms that mean that cells can only grow for so long, and then they fade and die. To grow a cancer cell, it has not only to corrupt the normal plan for its behavior, but also side-step the 'die now' mechanisms pre-programmed into its DNA. One of those is the erosion of the telomeres which we mentioned in the last chapter—cells run out of telomeres if they grow for long enough, and need to mutate in a very specific way to get them back again. There are also signals from other cells that can trigger cells to die, and our emerging cancer must evolve a way to overcome them.

The system is not perfect, of course, otherwise cancer would be a rare disease indeed. But it works well enough to keep nearly every one of maybe 20,000 trillion cells working for the good of the overall organism.

Although semantically there is a clear distinction between a unicellular and a multicellular life form, in nature the distinction is less clear. Some organisms like myxobacteria (whose fascinating biology we will describe a bit later) can revert back and forth between unicellular and multicellular life stages. Many single celled organisms cooperate with each other in 'the wild' to some degree, even if they are of a different species. This may include clumping together, forming colonies, forming a symbiotic relationship, or some other type of cooperation. So there is a gradient of multicellularity, from simple, single cells living on their own to communities of single cells, aggregates, through organisms that can switch between a unicellular state and a multicellular state to our own type of life.

The organisms that can switch are particularly intriguing. Are they unicellular or multicellular? These organisms, termed facultative multicellular organisms, have to be classified separately, as they are distinguished from those organisms that cannot switch back to a unicellular life style. The latter ones are termed obligate multicellular organisms. Facultative multicellular organisms have much greater flexibility. Their cells maintain a close cooperation only as long as it is needed or environmentally favoured. A single cell of an obligate multicellular organism cannot reproduce or survive on its own, and obligate cells have no choice but to cooperate in order to survive. This locked-in cooperation can be highly beneficial, allowing increase in size and specialization. However, it also includes high risks, because either the whole collective of cells survives or dies.

Environmental stress can be a driver of multicellularity. In a stressed and declining population, advantageous mutations will spread rapidly. There are two options: cooperation or competition. While competition is usually emphasized as the dominant biological process, with the mantra of "survival of the fittest", cooperation is often underestimated. There are many examples in biology of cooperation, extending from cell aggregates, biofilms, colonial life styles, and symbiosis, to eventually obligate multicellularity as the pinnacle of cellular cooperation. The great advantage of multicellularity is that the energy an individual organism expends can be optimized, and indeed multicellular organisms are known to transform more energy per unit of biomass than unicellular organisms. Additionally, if organisms can cooperate, they reduce the amount of effort (energy and material) they need to put into competition. So it is under environmental stress, when resources are limited and organisms need every bit of energy just to survive, that individual barriers are most likely to fall in exchange for a way of closer cooperation. One of the best examples is *Ectocarpus siliculosus,* a brown alga, which is multicellular and tends to inhabit intertidal zones. These ecological niches are notorious for the constant and intense abiotic and biotic stresses, due to both the tidal change and the dense biota.

Although the evolutionary step from a single-cell to a multicellular organism is generally considered to be one of the pinnacles of life's march toward increasing complexity and is one of the critical transitions for our hypothesis of a universal Cosmic Zoo, only a small fraction of organisms have chosen the pathway to multicellularity. Life on Earth is still dominated by single-cell organisms, both by numbers and by total biomass. Further, not all multicellular organisms achieve a higher degree of complexity than unicellular organisms, as is nicely demonstrated by *Erythropsidinium*, a unicellular dinoflagellate that commonly occurs in plankton (Fig. 8.1). This single celled organism has a flagellum for moving, a nematocyst—a specialist structure with which it spears its prey, a gut, even an eye. In some respects it is more

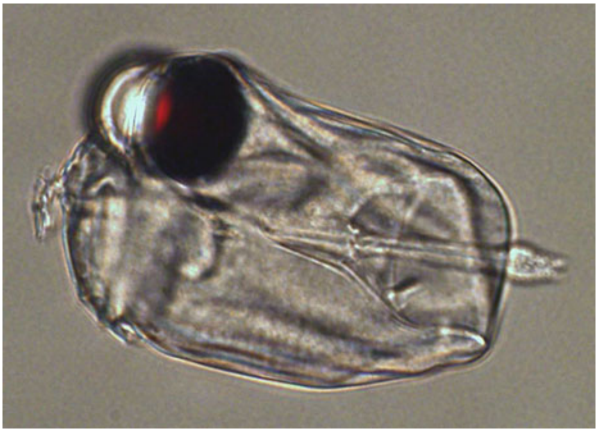

Fig. 8.1 *Erythropsidinium*, a unicellular dinoflagellate, with a structure similar to an eye. This structure is called an ocelloid. Image is courtesy of Fernando Gómez

complex than a sponge or a coral, which cannot move and does not have an eye. Could even more complex single celled organisms exist? Is multicellularity the only route to achieve a truly complex organism? Are there multicellular bacteria?

8.2 Multicellularity and the Domains of Life

There are three domains of life: archaea, bacteria, and eukaryotes (Box 1.1). All three domains of life have achieved a quite amazing level of complexity, with some evolutionary innovations comparable to multicellular accomplishments; but only eukaryotes have evolved true multicellularity—meaning, in this context, obligate multicellularity.

Bacterial multicellularity has been claimed for certain groups such as cyanobacteria, actinobacteria and proteobacteria; and indeed some of these organisms are facultative multicellular, but do not exhibit full (obligate) multicellularity. Some types of cyanobacteria form long filaments containing specialist cells for fixing nitrogen and for forming spores. They are doing what a multicellular organism can do, forming several cell types from a single genome. But they only form a very limited number of cell types, and can turn this ability on or off depending on the environment. They can live fine as single cells. They are therefore facultatively multicellular, and not very complex at that.

A more intriguing example is the myxobacteria. Myxobacteria belong to the phylum of the proteobacteria, to which some of the famous pathogens like *E. coli* and *Salmonella* belong, but also many other genera. Myxobacteria are rod-shaped bacteria, which live in soils worldwide and feed on insoluble organic compounds. They excrete a sugary slime when they intend to move, which they accomplish by gliding, and so they are also known as slime bacteria. Myxobacteria live under oxygen-rich conditions and are able to form mobile, predatory swarms, also known as wolf packs, enhancing their feeding efficiency. However, when faced with starvation, a large number of swarming cells form aggregates and lose their individual behaviour. Masses of cells firmly stick together, and 60–95% of the cells in the mass get destroyed by their own enzymes. Finally, the unstructured mound of cells develops a distinctive, organized shape called a fruiting body, with defined structural elements such as a base plate, a stem, and a wall with spores (Fig. 8.2). Once the multicellular development to form a fruiting body is initiated, it occurs within several hours, indicating that myxobacteria have acquired a distinctive development plan. The spores are then released, and disperse in the air or water. The spores are

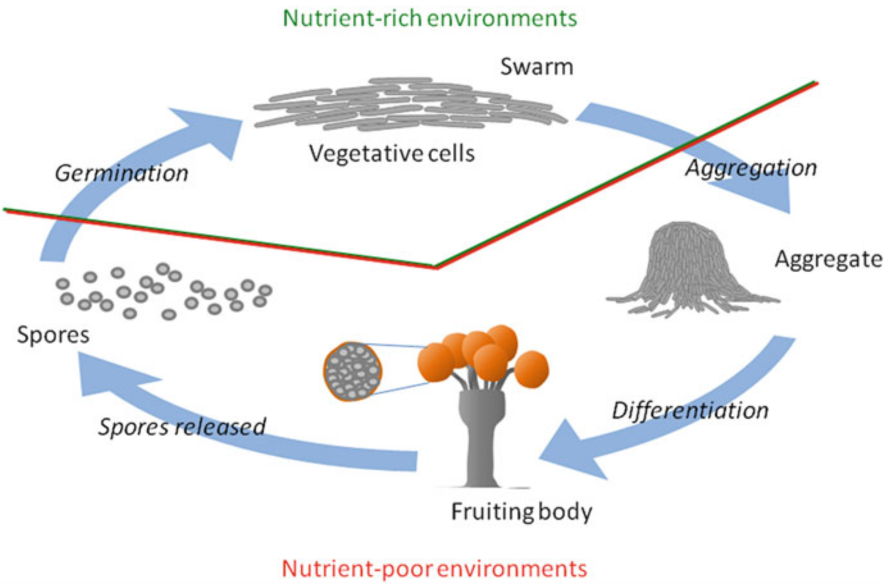

Fig. 8.2 The myxobacterial life cycle

dormant forms of a cell that can stand high UV irradiation, drying out and other conditions that would kill the ordinary bacterial cells. Once the spores come into a nutrient-rich environment, they germinate again and form individual vegetative cells that can again "hunt" in swarms.

However, the myxobacteria are not obligately multicellullar, because the multicellular stage is not strictly necessary for their continued existence (the individual cells can also reproduce by binary fission). The multicellular stage is triggered by an environmental cue, as is the differentiation of the filamentous cyanobacteria. Myxobacteria present a striking example of a potential step along the path to obligate or true multicellularity, but they haven't quite achieved it, because the multicellular phase is transitory in nature. Obligate multicellularity, on the contrary, requires any organisms no choice of being multicellular.

Even this level of complexity requires a program, which means more genes. Interestingly the myxobacteria and the filamentous cyanobacteria have the largest genomes of any bacteria, 9–10 million bases (as opposed to a typical bacterial genome of between 1 and 5 million). But this seems to be the limit for bacteria. We will discuss why this might be in the next chapter.

While the myxobacteria are unusual in forming large, genetically programmed structures on their own, collaborative behaviour which builds large structures is not unusual in bacteria or archaea. There are structures that have been identified in archaea and been interpreted to be of multicellular nature. Well-known are the associations in oxygen-poor marine sediments of archaea and bacteria, which belong to two different domains of life. However, these collaborations resemble symbiotic relationships rather than multicellularity. The same can be said about biofilms that are produced by some archaea and many bacteria when exposed to environmental stress. The secreted biofilms consist of proteins, sugars, and metal ions and salts, and perform the function of a protective barrier and as a reserve for nutrients. In this sense they constitute a common stress response, which is exhibited by many other bacteria. But there is no cell specialization in these films, so this is not multicellularity.

No bacteria have been found that have obligate multicellularity, i.e. in which cells of a multi-cell entity *have* to have different phenotypes based on the same genotype. Obligate multicellularity is observed only in eukaryotes. It is observed in many different branches of the eukaryotic domain. In some, all the members of that branch are multicellular, like the vascular plants and the animals. However, there are also branches of eukaryotes that are all unicellular like microsporidia (a group of parasitic fungi) and nucleariids (a group of amoebae).

Furthermore, there are branches of the eukaryotes that include both unicellular and multicellular species. Intriguingly, this does not occur only at the phylum level, such as for fungi, but also on a much lower hierarchical level as is exemplified by the Saccharomycetaceae, a family of yeast that reproduce by budding. The family includes the famous fungus *Saccharomyces cerevisiae*, the organism commonly called “yeast” because it is the species of yeast used for making bread, beer and wine (although, in fact, there are many species of yeasts). *Saccharomyces cerevisiae* is clearly unicellular, while the quite closely related filamentous cotton pathogen *Eremothecium gossypii* is an obligate multicellular organism. The same family also includes *Candida albicans*, known to cause oral and genital infections in humans, which is capable of switching rapidly and reversibly between unicellular and multicellular life styles. *Candida albicans* is a facultative multicellular organism comparable in complexity to the multicellularity achieved by many of the bacteria, such as myxobacteria. The switch between life styles is triggered by environmental cues, and may be interpreted as an indication that what most of us usually consider a monumental evolutionary step may be achieved quite simply by these life forms, at least on a functional basis.

8.3 What Was the Evolutionary Path Toward Multicellularity?

So there are different degrees of cooperation within the microbial world, from loosely cooperating cells to very closely cooperating cells, like myxobacteria, which cooperate so closely that they can be considered multicellular during some part of their life cycle. As often in biology, there is so much diversity in both organisms and life cycles that the identification of the critical step is not necessarily straightforward. The result is a disagreement by scientists of what the critical transitionary step actually is. We think that identifying the deciding step is quite clear; it is the achievement of obligate multicellularity. Once that step is passed, multicellular organisms are locked into a state where the choice between a single-cellular and multicellular life style is no longer possible. This is a conceptually monumental shift in life strategy, because division of labour between cells has been incorporated into the genetic program of the organism. Reverting to a unicellular life style is not an option. It is cooperate to the fullest extent or die. This means that organisms are free to develop cells like the nerve cells of animals or the phloem cells of plants that are so highly specialized that they could never survive on their own, but which allow large, complex organisms to develop.

But how was obligate multicellularity achieved? Scientists still argue about this, but there seem to be at least three different paths to the emergence of a true multicellular organism: colonial aggregation, incomplete cell division, or by a genetic split.

Many scientists suggest that the path to a fully multicellular life form was achieved through some type of colonial aggregation (Fig. 8.3). This speculation is reasonable, because various types of unicellular life, which are often closely related, form agglomerations and coordinate their survival strategies when faced with environmental stress and starvation. The formation of these aggregations enhances the survival potential of the aggregates compared to the chances of an individual—similar to the strategy used by a flock of birds or a school of fish. Once the environmental stress conditions ceased to exist, so would usually the agglomeration; but once in a while the aggregations develop into something more than a simple association. An example are fruiting body structures, where cells adopt a specialized function within the colony, and thus reach the level of a facultative multicellular organism. The lifestyle of the organism switches between unicellularity and multicellularity depending on the environmental conditions, which increases the likelihood that a genetic program will develop for both circumstances. If the environmental stress is

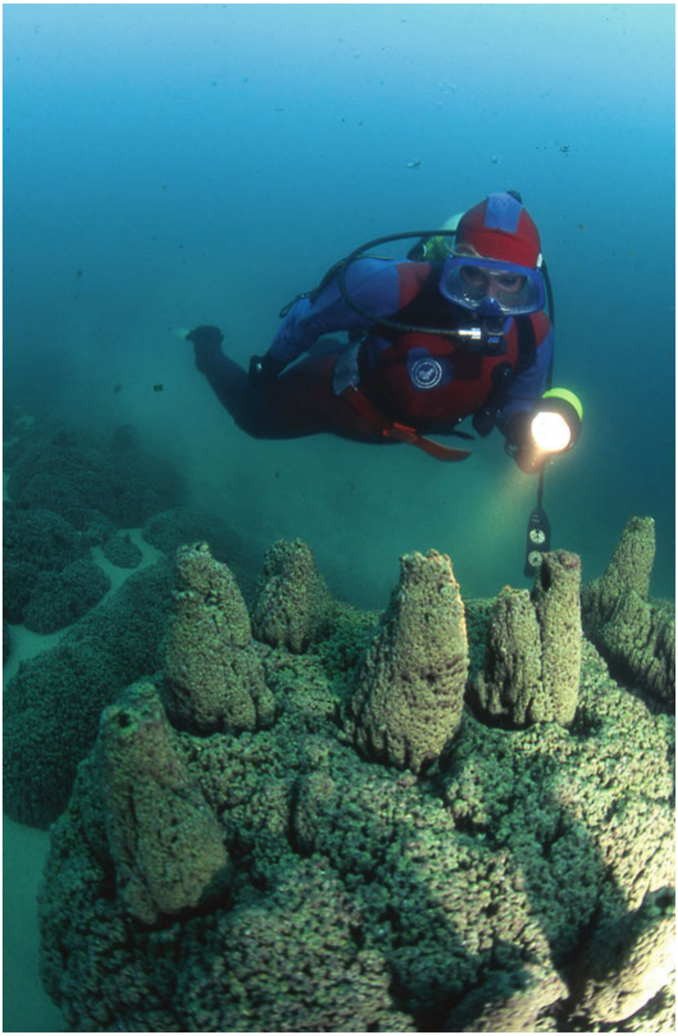

Fig. 8.3 Colonial organisms (microbialites) at Pavilion Lake, Canada. They build structures and have functional properties reminiscent of sponges. Credit: Courtesy of Donnie Reid (c) 2017

persisting for a long time, it is suggested that it would be energetically advantageous for the organism to suppress, skip, or drop the unicellular program altogether, and just go with the multicellular program and life style. Once it is always in a multicellular state, mutations could occur that prevented the cells ever surviving as single cells again. Once that 'ratchet' step had been taken, the organism would be an obligate multicellular species.

A boost for the colonial theory of the origin of multicellularity for animals comes from the choanoflagellates. These are a diverse group of aquatic eukaryotes that prey on bacteria. All of the more than 125 choanoflagellate species described so far are unicellular, with some of them being colonial organisms. No multicellular choanoflagellate has yet been identified, but many scientists consider them to be the closest unicellular ancestor to animals. The assumed close association to animals is based on genome sequencing and the signaling proteins that choanoflagellates use when their cells clump together, which otherwise only animals possess. Since some of the choanoflagellates have a colonial lifestyle, the implication is that the pathway to multicellularity might have passed through colony forming cells. Indeed, choanoflagellates closely resemble choanocytes, cells that line the interior of sponges, but which are also found in some other animals such as ribbon worms. Choanoflagellates even have p53, the cancer-fighting gene in humans, and associated transcription factors, for which there is no obvious role in these organisms. p53 is closely linked with the genetic program that, in animals, causes cells with DNA damage to kill themselves in an orderly fashion rather than risk that the DNA damage will continue and turn them into cancer cells. For a single-celled organism, or even a simple colony, such a program makes no sense, which suggests that choanoflagellates might be more cooperative and nearer to true multicellularity than is obvious (although, in an alternative explanation, p53 might play some other role in these organisms). It is another hint that the path to multicellularity might have arisen via closely cooperating colonial organisms.

Another pathway to multicellularity may be incomplete cell division, which happens quite frequently in biology. Two cells divide, but do not completely separate, and so the mother and daughter cell remain attached. Given that they are related (genetically identical, in fact), it is worthwhile to cooperate. The more they cooperate, the more likely they are to survive their accidental linkage. This could lead to a division of tasks. If there was a genetic reason for the physical linkage, and if that can be transmitted and re-inforced in subsequent generations, then the result is an obligate multicellular organism. The task separation could have occurred already before the incomplete cell division or may have occurred afterwards. Either way, cells which are developmentally locked into that type of cooperation with their clones become less able to 'escape' to live on their own, which will reinforce the benefit of future mutations that confer greater specialization and cooperation on the cloned cells.

These two paths are based on what was two cells (and then more) becoming one organism, The third is the reverse—one single-celled organism becoming multiple cells. Some of the microorganisms that are positioned at the unicellular—multicellular transition may provide us with some hints as to how true multicellularity was achieved eventually. First, there are the ciliates to which *Paramecium* belongs—an organism widely used in classrooms and laboratories to study biological processes (Fig. 6.1). *Paramecium* is a prime example of how complex a unicellular organism can become. *Paramecium,* like other ciliates, has two nuclei in one cell—a micronucleus which is essential for reproduction, and a much bigger macronucleus, which controls the non-reproductive cell functions such as metabolism. If a cell wall was to evolve between the two nuclei, we would justifiably categorize *Paramecium* as an obligate multicellular organism, because both cells would have different functions—indeed *Paramecium* would have germline-soma separation. In practice, given the interdependency of both nuclei, a cell boundary would easily disrupt the communication and cause a total collapse of the organism. Thus, it would be very unlikely that such a boundary would appear in *Paramecium.* Nevertheless, in some rare circumstances the organism might survive an internal division, adapt, and transmit the innovation to the next generation. If that would occur, the resulting organism may be comparable or even exceed the complexity of sponges, of which some also only exhibit two types of cells.

If these early steps to multicellularity are evolutionarily simple, can we see them happening today? We can in a quite spectacular way, in laboratory experiments. While the transition to complex, obligate multicellularity with clearly differentiated cell types occurred over millions of years, the first crucial steps in the transition from unicellularity to multicellularity can occur in very little time. William Ratcliff from the University of Minnesota and colleagues demonstrated that the first crucial steps toward multicellularity can occur within 15 generations. They showed that by altering a single gene in the yeast *S. cerevisiae* that controls separation of cells produced by cell division, the yeast cells would clump together to form a structure similar to a snowflake. As the snowflake structure would grow further at the individual branches, later mutations would be confined to the branches only. Thus, the yeast would undergo evolution like a multicellular organism, not a single cell.

Matt Herron experimented with the green alga, *Chlamydomonas reinhardtii*, a species with no multicellular ancestors, and found that when he exposed the alga to a natural predator, which preys on unicellular algae but not multicellular ones, that the algae evolved multicellular properties within 600 generations. The multicellular properties also included rounded shapes, typical for naturally multicellular algae. Based on his experiments, he suggested that the transition to multicellular life does not only depend on the nature of the unicellular ancestor, but also on the specific selective evolutionary pressures driving the transition. While none of these experiments demonstrated the division of labor observed in fully multicellular organisms, such a division would be expected to develop by natural selection eventually.

8.4 Multicellularity on Earth and Other Planets

We have seen from the ideas above that the evolution to multicellularity does not appear to be a distinct step, but more a continuous hill that was climbed on the way to increased complexity. How likely is that to occur?

Only eukaryotes can be obligately multicellular. We discussed the appearance of eukaryotes in Chap. 6, and argued there that the appearance of complex cells, either by endosymbiosis or interior partitioning, is a Many Paths process. In this chapter we have argued that the steps along the way to multicellularity are apparently relatively simple. Note that we are not saying that any of these steps are 'easy'—they take the accumulation of many genetic changes. But there are many combinations of genes, Many Paths, that can result in that endpoint, and so given time it is likely to happen.

With these two pieces in place, we can say confidently that multicellular life is common, indeed almost inevitable, because it has arisen many times. If that is so, we would expect multicellularity to evolve multiple times on the Earth. And it has.

Many distantly related branches of the eukaryotic tree of life hold multicellular life forms. In particular, these include Ophistokonts, and plants. The Ophistokonts are a diverse group of organisms that include animals, all of which are multicellular, uni- and multicellular fungi, unicellular microsporidia (also a type of fungi), and choanoflagellates. Within the Ophistokonts, it is clear that multicellularity evolved at least twice, in the ancestors of fungi and animals. Genetic data suggest that these two ancient lineages [technically the holomycota (which include fungi) and the holozoa (which include animals)] diverged long before there is any evidence of multicellular life on Earth. Thus the originating organisms at the base of the fungal and animal branches were almost certainly unicellular, and multicellularity evolved independently in fungi and animals. It also evolved independently in the plants, whose ancestor diverged from the Ophistokonts not long after the eukaryotes evolved. It is believed likely that land plants and algae evolved multicellularity separately. The plants and fungal groups contain species that are unicellular, others that are facultative multicellular that can easily switch to and fro between unicellular and multicellular life styles, as well as true, obligate multicellular organisms.

Based on what we know from life on Earth, it thus has to be concluded that the transition from unicellular life to multicellular life will inevitably be mastered elsewhere by biology given similar evolutionary pressures. The evolution of consumers (organisms that feed on other organisms, such as animals) seems inevitable once a sufficient number of primary producers (such as plants) is available in an ecosystem. The total biomass would become larger and increasingly complex. A consumer has the advantage of deriving energy directly from organic building blocks rather than having to convert energy from the abiotic environment. An increase in size would provide an organisms a critical advantage, for a producer (prey) to avoid being eaten, and for a consumer (predator) to be able to eat the producers, and for both to produce more specialized tissues and organs for feeding, and then for sensing, movement, defense and reproduction. The easiest way for the first consumers to eat the producers was simply to engulf them as food, for which size was critical (see also Chap. 6). With the evolution of a higher level consumer which would also be able to eat other consumers, a virtual arms race would ensue, further increasing natural selection pressure on size.

The same forces will apply on any other planet given sufficient time and adequate habitat conditions to allow for complex ecosystems to evolve. Starvation will always be a challenge, and prey and predator relationships, and the evolutionary pressure to grow larger are also to be expected on other planets given a sufficient biodiversity and biomass.

The transition from unicellularity to multicellularity occurred many times on Earth, and many transitional forms are still around today, from colonial organisms such as microbialites (Fig. 8.3), to facultative multicellular organisms such as the myxobacteria (Fig. 8.2), to fully multicellular organisms such as sponges (Fig. 10.4). Not only has the transition on Earth occurred many times, but the innovation of multicellularity has evolved recurrently in different distantly related species. Thus we have to conclude that the transition to multicellularity must be a Many Paths process that will inevitably occur given sufficient time and suitable environmental conditions.

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9

The Rise of Complex Animals (and Plants)

So far in this book we have argued, we hope persuasively, that many things possessed by complex organisms such as ourselves—eukaryotic cells, multicellularity, sex—and things we depend on, such as oxygen, were likely outcomes once life was established on Earth 3.5 billion years ago. But we have scarcely mentioned the appearance of large organisms themselves. What about molluscs and dinosaurs and trees?

9.1 Larger Size and Complexity

The path toward multicellularity which we discussed in the previous chapter was also related to size. Multicellular organisms usually reach a larger size, which has a number of advantages. Single cells have physical size limits, because the larger the cell the larger will be the diffusion distance from the cell membrane to the cell center and the more dramatically the surface to volume ratio of the cell will drop. Both constraints will make it much more challenging for the cell to take up nutrients, expel waste, and coordinate the various functions that a living organism needs to execute. Thus, the obvious solution to circumventing the constraints on cell size imposed by physics, yet still to grow in size, was to become multicellular, with transport pathways in between cells.

Large size also enables you to escape the surface stagnant boundary layer. The water right up against a surface is always virtually still, even if the bulk of

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water in a stream or a river is flowing. So a small organism such as a bacterium on a surface has to rely on diffusion to bring nutrients to its cell's surface. If you can stick up out of this boundary layer, say a whole millimeter into the bulk of the flowing stream, a supply of new nutrients washes past you much faster. This helps you gain a better nutrient supply, especially in times of scarcity. Really large organisms, like insects or elephants, are also buffered against temperature. A large organism can develop a specialist outer skin or shell to protect against dehydration, UV light and, of course, attack from other organisms. Organisms with more cells can have more specialized types of cells, and more of them to develop more sophisticated responses to the environment. This suggests that in organisms that can have a range of sizes, larger organisms might be associated with more specialization.

There are not that many organisms that are multicellular and yet can vary their size and their level of specialization, but the colonial algae provide an example. The colonial green algae of the genus Volvox, which lives in a variety of freshwater habitats, forms spherical colonies of up to 50,000 cells. Volvox can reproduce sexually and asexually and differentiates between somatic cells and germ cells, a distinct attribute of a multicellular organism. In one species of the genus, *Volvox carteri,* this differentiation was shown to be defined by size. If the cell was <8 micrometer in size, the somatic program was activated; if larger than that, germ cells began to be produced. Larger size was linked to greater specialization.

Once you have multiple cell types, large size can itself support more flexible function. Both the mammalian immune system and the mammalian brain have individual cells that specialize in specific functions, and (broadly speaking) the more cells they have the more capable they are. For organisms that do not move, large size enables them to spread into new territories to gain nutrients, while not abandoning their original niche.

Not all of these features are advantages to all organisms, of course. Multicellularity and large size is one specific evolutionary and ecological tactic among many. The majority of eukaryotic groups are single celled, and of course all bacteria and archaea are single celled. But for some, large size is a selective advantage (Box 5.1). However, to arrive at animals and plants, and eventually us, more than simply large size is needed. Instead complexity is the critical parameter. A mouse has about the same complexity as an elephant although it is much smaller, and huge corals are not more complex than plants. So how do we evaluate the complexity? One approach is to choose the number of cell types. For example, a sponge has as little as two cell types, a human about 200. Another approach, for which will argue below, is the number of steps in the genetic development program. But before we do this, let's turn to the time period of Earth's life history in which the diversity of body plans and shapes of animals and plants skyrocketed—the time period starting about 540 million years ago, which is referred to as the Cambrian Explosion.

9.2 The (Slow-Burning) Cambrian Explosion

One of the most singular transitions of life on Earth from a human point of view has been the Cambrian Explosion. The "Cambrian Explosion" is the phrase coined by palaeontologist Stephen J, Gould to describe the appearance of animals in the fossil record 541 million years ago. For fossil hunters from Victorian times to the end of the Second World War, the earliest known fossils were those in the Cambrian period, a stretch of time from 541 to 485 million years ago (Box 1.2). At the start of the Cambrian, a whole range of fossils appeared in the rocks, including ancestors of many types of animals alive today as well as ones now extinct like trilobites and the weird animals of the Burgess Shales. Before the Cambrian—nothing. It looks as if, from some hidden beginnings, complex life just exploded on the planet.

In fact, it is not that simple. We now know that the 'explosion' took 10–20 million years to happen. And for at least 60 million years before the Cambrian Explosion the world was populated by the strange soft-bodied Ediacaran animals (Fig. 9.1). These simple creatures are like nothing alive today. They were flat discs, fronds and cabbage-like creatures, some of which moved slowly across the seafloor eating the bacteria and algae that grew there. But they had no shells, no skeletons, and so their fossils are extremely difficult to spot—they were not recorded as real animals until 1946. Since then it has been found that they were on the Earth from about 635 million years ago, and may have been present earlier. In the Cambrian they faded from view, may be because they were out-competed by the organisms that followed them that had legs and shells and teeth, but traces of them remain in some places into the Ordovician, 488–444 million years ago. The Ediacaran animals might have lived on Earth for about 120 million years, which would be nearly twice as long as separates us from the dinosaurs (Box 1.2).

So something started to happen about 635 million years ago that culminated in an explosion of new animal types by the start of the Cambrian Period, about 541 million years ago. What was it, and—critically for our quest—was it a uniquely unlikely event or was it something that we would expect to happen again if we re-ran the Movie of Earth? To understand this, we have to understand what it takes to make an animal.

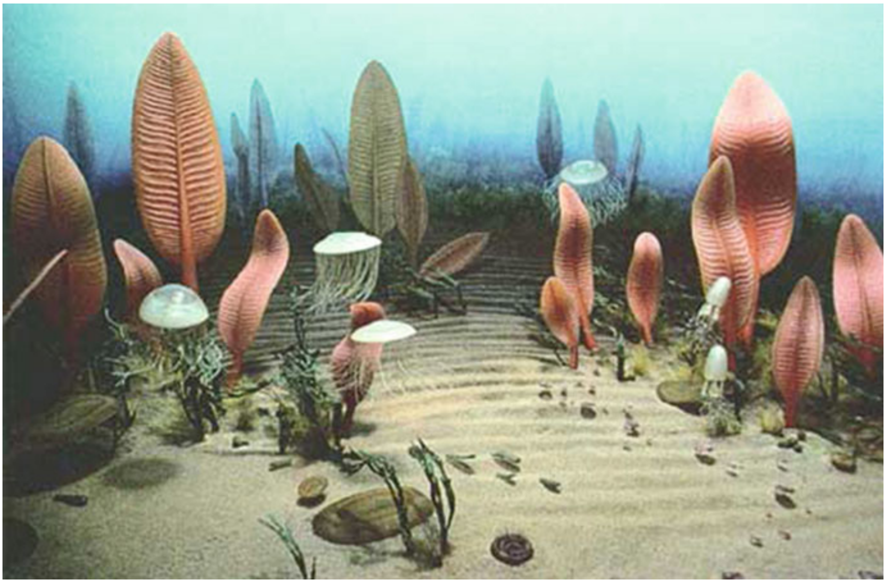

Fig. 9.1 The Ediacaran Fauna, soft-bodied animals that lived before the Cambrian Time Period, about 600 million years ago. Courtesy of the Department of Paleobiology, National Museum of Natural History, Smithsonian Institution

9.3 How to Build an Animal (or Plant)

There are two requirements for making a complex organism such as an animal or a plant. The first and most basic is that the organism has to be able to grow and reproduce. For cells that can survive on their own, like all bacterial cells, reproduction is simple—a cell divides, and daughter cells are all capable of independent life. But for a more complex organism such as a jellyfish or a seaweed the cells cannot survive on their own. Individual organs or tissues cannot survive. All the cells must be built and assembled into an organism before it is launched into the world, and the cells and tissues have to be assembled in the right order. It is no good building the lining cells of a gut before the basic structure of the gut is in place. The nerves linking the eye to the nervous system have to form when the brain and eye are forming, or they have nothing to connect. So the developmental program for a complex organism is going to describe how to build many cell types—a dozen in the case of a tree, hundreds in the case of a mammal—and build them in the right place and the right time.

Cells must also move, grow and die at the right time. Cells move around a lot during our development, interacting dividing and dying, all under precise control. Ultimately this is coded in the genes. Study of the genes that code development, and how they evolved, is the relatively new field of Evolutionary Developmental Biology, snappily called EvoDevo. It is to the genes that we turn for one explanation of the Cambrian Explosion.

Many genes that are involved in the development of a complex organism have been discovered, often starting from studying mutations in the fruit fly *Drosophila melanogaster*. Geneticists have found many mutants that result in flies that develop abnormally—for example, failing to develop the right number of segments in their thorax (the central section where the wings grow), developing stunted body parts, or even more bizarre mutations such as those that grow legs where their antennae should be. A group of these genes are called the Hox genes. Hox genes are responsible for aspects of programming the front-to-back pattern of the body, so mutations in them cause body parts that are usually formed in a specific place along the body (such as wings, legs) to be malformed, or formed in the wrong place. Hox genes help define the body's overall pattern of parts in all of the Bilatera, the animals that are symmetric left-to-right but have distinctive front-to-back and top-to-bottom patterns. We are members of the Bilatera, as are all other vertebrates (animals with backbones), insects, and flatworms, nematodes and many others. Jellyfish are not Bilaterans, because they have a distinctive top-to-bottom axis but not an obvious left side and right side. The same is true of sponges.

However the Hox genes are also present in sponges and jellyfish. Indeed, every animal studied has a version of the Hox genes, suggesting that they originated no later than the common ancestor of humans and jellyfish, some 600 million years ago. Of course, in jellyfish Hox genes are not responsible to guiding the development of legs or antennae—jellyfish do not have legs. They must be doing something else, and their function in such primitive animals is the subject of much research. But our point here is that this is an ancient gene family, which has been adapted in complex organisms to tell the developing embryo where to put its parts along a front-to-back axis.

Other developmental gene families have been shown to be even more ancient, and may well date to before multicellular animals evolved at all, which raises an odd question. If the function of a gene is to guide the development of a complex multicellular organism, what is that gene doing in a single-celled organism? The not entirely satisfactory answer is "something else", but this is a key insight. As molecular biologist Francois Jacob once commented, evolution is a tinkerer. New functions are not designed. They are put together out of whatever parts happen to be around. The whole developmental program is built from genes that have been co-opted from other functions. Usually this happens through gene duplication, a process we met before when discussing how photosynthesis evolved. A mistake in copying the DNA—a mutation—makes two copies of a gene, and subsequent evolution allows one to mutate and acquire a new function, leaving the other to carry out its old function. This results in genes forming groups of closely related genes, often called 'gene families'. The Hox gene family in humans has 39 members, genes that are all important for our development and all derived through duplication and subsequent mutation from one gene in our distant ancestor at least 600 million years ago. This has happened many times in many different gene families, it is clearly a very common way that evolutionary innovations arise, and is therefore a Many Paths process.

The resulting developmental process can seem odd. For example, the land vertebrate limb (like your arms or legs) starts out as a small bump of cells on the side of the early embryo, called a limb bud. Where the bud forms, and what sort of limb it will develop, is determined by genes that detect how far a cell is down the body of the embryo. The cells in the limb bud grow, extending the bud into a long extension. As it grows, other genes determine how far down the growing limb a cell is, and hence whether it is ultimately to form a hand, an elbow or a shoulder. Others say whether a cell is at the front or the back (if you interfere with the patterns of signals between cells that allow front-and-back discrimination, the result is abnormal limbs that look like they are trying to develop two thumbs, because both cells at the front and the rear of the limb are acting as if they were at the front). As the limb develops it develops bulges at the end furthest from the body that will develop into the five fingers characteristic of all land vertebrates.

So what of land vertebrates like horses, which do not have five toes on each foot? They follow the same path, but then early in development the cells that are going to form 'toes' that are not wanted die off. Rather than build a one-toed limb from scratch, evolution has built a five-toed limb and then removed four toes. The same is true of how the five toes are made in the first place. The vertebrate limb gets cells to die off in bands along the end of the growing limb, leaving five extensions that become fingers or toes or hooves.

So the dance of genes and cells in development can be extremely complicated, and not at all the way an engineer might design it. But it works, genes such as Hox and thousands of others are making the right cells at the right place and the right time.

This suggests that there is more to the story than the genes themselves. It is also about how they are deployed.

9.4 The Genetic Blueprint of EvoDevo

One of the surprises of the human genome project was that humans only have a few more genes that make proteins than does *Drosophila*, and only about 5 times as many as *E. coli*. This shock to our self-esteem has been mitigated in the last decade by the realization that most of the DNA in complex organisms is related to how genes are controlled, not to how they make protein. It used to be thought that most of the genome of mammals was 'junk DNA'. It is now realised that some, maybe quite a lot, of this 'junk' was in fact important for the control of genes, and we just did not realise it.

Why is gene control central to EvoDevo? Surely the important molecules are the proteins that control cell shape and function, and DNA is important because it codes for those proteins. Yes and no. Yes, a single base change in DNA can cause protein malfunction which can cripple an organism. But getting those proteins made in the right cells, the right tissues and at the right time requires a complex control system, and that, it turns out, is what a lot of our extra DNA is for. Those complex control systems allow the egg to contain the program that ultimately builds a complete adult human being over a period of 20-odd years.

This is not to say that environmental influences are not also critical. Genes program cells to act in response to their environment, which always includes other cells. If the environment changes, then their behaviour changes. If the environment changes so much that it is now outside the range of environments that the genes were evolved to respond to, then the system breaks down. This is what happens in Fetal Alcohol Syndrome. Dosing a growing embryo with lots of alcohol was something the genes were never evolved to cope with. But if the environment is not too different from that for which the genes were programmed, then a new, healthy individual will result.

So eukaryotes' more complex genetic control systems are a key to the ability of some eukaryotes to evolve multicellular organisms. We should emphasise that most types of eukaryotes are not multicellular. There are many types of eukaryotes that are single cells, such as the protozoa that Antonie van Leeuwenhoek saw when he first used a microscope on a drop of pond water. As we have seen already, protozoa (more properly, protists) can have extremely complicated cells, again using complicated genetics, but are single cells. But in this book we are focusing on the path to complex, multicellular life, so let's follow that evolutionary line.

Acquiring genetic complexity is now seen as one of the key transitions on the way to complex life. But how likely was it?

9.5 Gene Control in Eukaryotes

Eukaryotes have far more elaborate gene control systems than prokaryotes. As we have mentioned, prokaryotic cells such as bacteria contain their chromosome as circular DNA. Usually the entire genome is a single circle. In all cells DNA is wrapped up into a compact package using proteins. There is an entirely practical reason for this. The circular chromosome of gut bacterium *E. coli* is 4.6 million bases long, and would be a circle about 1.4 millimeters round. That has to fit into a cell about 1/1000th that size. The two sets of 23 chromosomes in each of your cells would stretch out to ~2 meter if lined up end-to end, but has to fit into cells an average of 10–20 micrometers across. All the DNA in your body, if lined up end-to-end and fully stretched out, would reach from Earth to Pluto 17 times. Obviously, this needs some packing. In bacteria, the DNA is packaged by DNA-binding proteins in loops, which are concentrated in part of the cell called the nucleoid. However, it is not separated from the rest of the cell by a nuclear membrane as in the eukaryotic cell. In eukaryotic cells, the DNA molecule is also packaged around proteins, called histones, that compact its structure. These are themselves packaged with more proteins, and the whole is wrapped inside a double membrane to form the cell nucleus.

Genes are controlled by turning on or off the enzymes that make RNA from the DNA template. There are multiple types of control of gene activity in eukaryotes that overlap with each other. The different control functions have evolved many times with the same general type of genetic function often being carried out by different chemistries in different organisms. Many types of control chemistry in eukaryotes have precedent in bacteria or archaea.

For example, small RNA molecules are involved in gene control in all domains of life, and have evolved independently at least twice in eukaryotes. Of course, the precise mechanism and molecules concerned are different, so the specific molecules made in eukaryotes are unique. For example, in eukaryotes there are a set of small RNA molecules called piRNA, which work together with a set of proteins called Piwi proteins to target yet other proteins to specific sites in DNA and chemically modify the DNA molecule. All this complexity is unique to eukaryotes.

But the general principle of changing the chemistry of DNA to control lots of activity is seen in all domains of life, and evolved independently in them. The basic chemistry of a combination of a small RNA and a set of proteins targeting DNA is widespread, and again has evolved many times. So while the specifics of how piRNA work are unique, the general principle is not—it is a Many Paths process. We have gone into this depth, and show that for many examples of control systems—types of switches if you like—that make up the complex genetic control of eukaryotes, analogies exist in prokaryotes. Often the eukaryotic switch has evolved more than once independently.

All these examples show that different chemicals are used to arrive at the same functional imperative, thus these pathways have likely evolved separately in different organisms, therefore constituting a Many Paths evolutionary process.

So eukaryotes can have much more complex genetic controls than prokaryotes, but have the same types of chemical function. So why are there not complex prokaryotes? Is there something unique to eukaryotes that we are missing, and whose evolution was possibly a unique, unlikely Random Walk event?

We think that there is a basal feature of eukaryotic genomes that allows this complexity, and prevents it in prokaryotes. Recall that DNA is packaged up into complexes with protein. That protein, and how it folds the DNA, is key to controlling DNA in all types of life. But how it works is subtly different in prokaryotes and eukaryotes not because of its chemistry but its arrangement.

Gene control systems are not computer code, no matter how much the language of molecular biologists talk of 'genetic switches' and 'genetic programs'. If the circuits of even a simple yeast's genome were coded in conventional computer language, they would be "Spaghetti code", a derogatory term computer programmers use to describe code whose flow is not a neat, well-ordered structure that anyone can follow, but is a tangled mess of instructions where it is almost impossible to work out what any change in the code would do. The different types and levels of control in the genome interact arbitrarily with each other to produce results that are chaotic. Of course, they *work*. If they did not, the organism would be dead. But *why* they work is one of the hardest things in biology to decipher. If we look at how all the proteins and genes in a cell are interacting with each other, rather than just looking at one protein or gene at once, it is found that every control system described interacts with every other.

This is a general feature of life, not just of eukaryotes, and is the subject of an emerging area of research called Systems Biology. This approach recognises that there is not a simple, linear path from gene to protein to function. Life is inherently complex, a network of interactions, what physiologist Denis Noble calls 'The Music of Life'. At the gene level, this means that the complexity of genetic control is not just a function of the number of genes and regulatory molecules. Rather, it is a function of the number of ways they can interact, which is a very much larger number. This is good news for the evolving eukaryote, *providing* it can work out how to get all those genes, regulatory

RNAs and proteins to work together. And *that* is the core problem that eukaryotes solved, and prokaryotes did not.

Let us say we want to create a new cell, with a new set of genes involved in that cell's activity. It was a well-known observation from the dawn of molecular genetics that most genes are not active in most cells of a multicellular body, nor in single celled organisms most of the time. So to create a new cell with new genes in it, we do not just need a set of genetic controls that will turn those new genes "on" in our new cell. We also need some sort of control that will "turn off" all the genes we do not want in that cell, and turn our new genes off in every other cell. We do not want a skin cell making eye lens proteins, or a nerve cell making haemoglobin.

The key difference between bacteria and archaea on one hand and eukaryotes on the other is not in how genes are turned *on* so much as how they are turned *off*. In prokaryotes genes are at a 'ready to go' status all the time. They are by default assumed to be 'on'. Adding a new gene is therefore easy. New DNA put into a bacterial cell will usually 'work'. By contrast, genes in eukaryotic cells are assumed to be 'off'. It takes a lot of metabolic effort to turn a gene on. So adding a new gene is harder, but making sure that it does not turn on in a cell where it is not wanted is already achieved. The more complicated the genome and the more specialised the cells, the more advantageous it is for genes to be by default 'off' and not 'on'. In our 2015 paper we thus arrived at the conclusion that the evolution of a genome in which the default expression status was 'off' was the key step that enabled the evolution of genetic complexity, and hence the evolution of multicellular organisms. This was the transition that allowed eukaryotes to evolve the complex systems that they show today, not the evolution of any single control system *per se*. This modification in how the genetic code is expressed was a critical advance for the continued evolution toward complexity.

Was this a Many Paths event? We do not know. Like the origin of life itself, this must remain an unknown in our hypothesis. But once it was achieved, the rise of multicellular organisms, and then organisms with complex developmental programs, was inevitable.

9.6 Oxygen and the Energetic Animal

We said at the start that complex, multicellular animals need two things, but we have only talked about one, the genetic control systems that allow the developmental program necessary for complex life. But this is not the only thing that may have triggered the Cambrian Explosion. The 'default off' genetics probably go back to the origins of eukaryotes, at least a billion years ago, yet the explosion of fossils in the rocks that form the Cambrian Explosion did not occur for another 450 million years. So what triggered the Cambrian Explosion? Many people believe that cause can be summarized in one word: *Oxygen*.

Today's animals, especially large, complex animals like you, need oxygen to power your high-energy metabolisms. Reacting sugars and fats with oxygen provides more energy than any other chemistry available to life. One example can show how beneficial oxygen is. Brewers yeast can live with or without oxygen. In the absence of oxygen, it takes glucose and breaks it down to alcohol, yielding 2 molecules of the energy-carrier molecule ATP in the process. In the presence of oxygen, it reacts sugars with oxygen to make carbon dioxide, and each glucose molecule yields up to 36 molecules of ATP, a 18-fold increase in efficiency.

Yeast are small organisms and they can get food fast by diffusion from the medium around them, and in times of low oxygen can simply throttle back their metabolism. Complex, multicellular animals cannot get their food by diffusion. They need to actively seek out food, either through energy-consuming molecular 'pumps' at the sub-cellular level, or with teeth and feet and fins to chase it. Those all require energy to power. They need a circulatory system to carry food to tissues a long way away from the food. And they need control systems to keep all this going. All this requires energy. This is why David Catling from the University of Washington has argued that oxygen is absolutely needed for complex life, and complex animals in particular only arose when the atmospheric oxygen level rose to levels seen in the latest part of the Precambrian time period, between 600 and 541 million years ago.

The Cambrian explosion happened at the same time as a dramatic rise in atmospheric oxygen levels occurred. In the late Proterozoic time period, which ranged from 1 billion to 542 million years ago, oxygen was maybe 1% of all the gas in the atmosphere, enough for yeast to use it, but not enough to keep a mammal alive. Then about 600 million years ago oxygen started to rise, and since the Cambrian time period it has been between 15 and 30% of the atmosphere (it is 21% today). For reasons we discuss in the next section, and have summarized in Chap. 2, it is hard to see how the oxygenation of the atmosphere could be accomplished on any terrestrial planet in less then 1 billion years. Of course, we have to be careful to not categorically exclude any possible shortcut solution to the required time scale, but our expectation would be that a planet has to be inhabited for a long time before high levels of atmospheric oxygen appear. If oxygen is absolutely necessary for complex life, then there has to be the same or a similar long wait on any planet or moon elsewhere in the Universe before complex life can arise.

We think this argument is over simplistic. Even today there are complex animals that can live perfectly well at 2% oxygen or less (i.e. only about 10% the modern level). Some animals like the Crucian carp can survive months in an extreme oxygen-deprived environments. Some sponges have been shown to survive, metabolise and even grow at 1% of modern oxygen levels. It is even claimed that some members of the phylum of the Loricifera, a type of microscopic animal that lives in between the grains of gravel and mud on the seafloor, do not need any oxygen at all. They were discovered, apparently alive and actively metabolizing, in the oxygen-free bottom sediment of the Mediterranean Sea. (This is controversial, as recently it has been suggested that the samples of these collected species were actually dead, and fell from higher, oxygenated waters, an idea the original authors have disputed). However it is clear that, even after adaptation for more than half a billion years to oxygen levels of between 15 and 30%, animal life can live with much less oxygen than is around in the air we breathe today.

Multicellular fungi can live without oxygen, and plants clearly can live without consuming oxygen, as they produce it, they do not consume it (during the daytime, at any rate—in the night they consume oxygen as we do, although not as much). Land plants can move (quite fast in the case of plants such as the mimosa or the Venus Flytrap), they have senses as fast and sophisticated as jellyfish or sponges, they have complex developmental genetics, and importantly they did not arise during the Cambrian explosion.

But whether oxygen is the critical enabler of the Cambrian Explosion or not is actually not that important to the story, because oxygen itself is probably the product of a Many Paths process as we touched on in Chap. 2, and are making the case for below.

9.7 Rusting Towards Animal Life

So if oxygenic photosynthesis evolved more than 2.4 billion years ago why did the Cambrian Explosion not happen then? Because there is a difference between oxygen being made and oxygen accumulating in the atmosphere. There are two reasons for this.

The ancient surface of the Earth has been full of minerals that can react with oxygen, making solid, insoluble oxides. Some of the most common were iron minerals, and as soon as oxygen was produced they would react with the iron and turn it, basically, to rust. We can see this in the geological record. Across the Earth thick layers of rock called Banded Iron Formations laid down in the early and middle of the Proterozoic time period (2.6–1 billion years ago) show the imprint of gradual oxidation of iron in the crust. Of course, erosion and volcanic action keeps adding more iron to the oceans, and that means more iron to react with the oxygen. It took nearly 2 billion years to oxidize all the iron in the crust. After that, oxygen made by cyanobacteria or plants would slowly accumulate in the atmosphere. Volcanoes push reduced gases like hydrogen and hydrogen sulfide into the atmosphere, and those react with oxygen too. One hypothesis suggests that the Earth's volcanism has gradually been declining with time, and around 600 million years ago the rate at which volcanoes produced oxygen-consuming gases was overtaken by the rate at which cyanobacteria and algae could produce oxygen. In either scenario, this was when the Vendian time period arrived, the Ediacarans started to evolve, and the path was laid for the high energy lifeforms of the Cambrian Explosion.

This process, the oxidation of the crust, is not a Random Walk or a Many Paths process. It is a Critical Path process. If a planet is making oxygen then ultimately its surface *will* end up completely oxidized. There is no chance involved, and the timescale is just defined by the amounts of rocks compared to the rate of production of oxygen.

We know this in part because it has happened before. Mars used to be a world with liquid water on its surface, probably even oceans. But the lack of a strong geomagnetic field to protect its atmosphere from erosion and its light gravity meant that the water tended to escape high into the atmosphere, where it was split into hydrogen and oxygen by UV light. The light hydrogen molecules escaped to space, some of the oxygen stayed behind and oxidized the surface. This is why the surface of Mars is red: it is rust-red from oxidized iron, and probably has been for more than 3 billion years. This is an example of a different path or mechanism for producing oxygen, in the case of Mars a completely geological one not involving life at all, but the result surprisingly superficially similar to the banded iron formations on Earth.

9.8 Head, Shoulders, Knees and Toes

So far, we have discussed the development of complex animals (and plants) in terms of general genetics and energy provision, but we have mentioned none of the marvelously complex structures that we see in animals today. When we wish to understand whether an animal as sophisticated as an elephant or a shark or a cockroach is likely to evolve on another world, we have all that complexity of anatomy and behavior in mind, not abstract questions of genetics. What of the heart or the eye or the immune system? What of wings or fins?

In fact, there are few examples of complex animal functions that have not evolved several times. Vision has evolved many times independently, in mollusks, insects, arthropods, tribobites, cephalopods and vertebrates. We know these are independent paths of evolution, because the anatomy of the eyes are different. Legs evolved independently in a dozen different lineages. Flight has evolved in the insects, birds, pterosaurs and bats quite independently. Specific aspects of particular functions seem to have evolved multiple times. Echolocation has evolved independently in bats, cetaceans, oilbirds and tenrecs (tiny shrew-like animals from Madagascar). The ability to locate a sound in space, to tell whether a car is approaching from your left or right, is seen in birds and mammals, but apparently birds and mammals use different neural systems to achieve sound location, which must have evolved independently. The ability to detect electric fields has evolved independently in fish (probably several times), the duck-billed platypus, bees and cockroaches. Long, jumping hind legs independently evolved in frogs, jerboas and kangaroos. The streamlined shape of marine predators evolved independently in sharks, cetaceans and plesiosaurs. The list goes on and on.

This is not just fine-tuning of a single developmental program. Modern molecular analysis suggests that more basic components of the body also evolved many times. Striated muscle (the sort of muscle that makes up your biceps and quads), evolved at least twice, once in the ancestors of the cnidarians such as jellyfish and separately in the ancestors to the Bilatera, animals which include insects and vertebrates. Hard body parts evolved multiple times, using different materials—chitin in insect exoskeletons, calcium phosphate in our bones, calcium carbonate in shellfish and sponges (almost certainly independently invented). Functionally, the immune system is a system of cells that defends against invading pathogens, and has the ability to 'remember' pathogens it has seen before so it reacts to them more aggressively the next time it sees them. The vertebrate immune system has a wealth of complex, unique features, but a functionally equivalent system has evolved from completely different components in jellyfish, and yet another, different defense system is seen in insects.

We could continue, but the point is clear. Once the ability to capture and use lots of energy for growth and movement has evolved, and once the genetic capability to program complex body parts evolve, then animals will evolve to acquire a huge range of functions as a Many Paths, highly probable process. All that is needed is an open ecological niche to fill, and time.

In conclusion, two things had to happen to allow the evolution of complex animal life: the rise of oxygen, and the invention of 'default off' genetics. Once both had happened, it seems that complex animal life evolved independently several times. The rise in oxygen seems to be inevitable after the invention of oxygenic photosynthesis (Chap 5), and in any case never limited the rise of the two other, independent groups of complex organisms; the plants and the fungi. The appearance of 'default off' genetics is more mysterious, buried in the origins of eukaryotes themselves. But once those pieces were in place, an explosion of animal capability was an inevitable, Many Paths process.

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10

Intelligence, a New Concept?

Humans, or at least the humans reading this book, pride themselves on their intelligence. Humans have by far the most advanced material culture and sophisticated, flexible communication system of any creature on Earth. But many animals show accomplishments that suggest substantial intelligence. So what is intelligence, and how likely is it to arise?

10.1 What Is Intelligence?

There are many definitions of intelligence, probably almost as many as there are of "life". Depending on the author, the focus of the definition has been put on problem solving, creativity, logic, understanding, abstract thought, memory, or emotional knowledge. Different definitions are used whether one human is compared to another, to different human subgroups or genders, whether artificial intelligence is contemplated, or whether different species are compared. A suitable definition in our case has to be as broad as possible and thus apply to all species, or at least to all known intelligent organisms. Walter Bingham defined intelligence as ability of an organism to solve new problems, while Walter F. Dearborn interpreted it as the capacity to learn or to profit by experience. Pei Wang defined intelligence as the ability for an information processing system to adapt to its environment with insufficient knowledge and resources. A more recent definition is the one by Louis Irwin and Dirk Schulze-Makuch, who defined intelligence in their 2010 book *Cosmic Biology*

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as the ability to integrate experience and anticipate the future so as to guide your actions. These definitions have some common themes.

We should distinguish between creatures that show “clever” behaviour because they are smart and have worked it out, and creatures that show complex, useful behaviour because they are pre-programmed. Bacteria alter their metabolism to produce enzymes that can digest the foods they encounter. How they do this was worked out in a classic series of experiments that earned French biologists Francois Jacob, Jacques Monod and André Lwoff the Nobel Prize in 1965. However, this process has little ‘memory’. The bacteria can never learn that (for example) every time they encounter lactose then they will encounter lactic acid an hour later. Even the smartest creature has pre-programmed behaviour. If someone blows a sharp puff of air at your eye, you will blink. There is no thought involved. We call this ‘instinctive’ behaviour, but that just means that there are specific nerve circuits that connect the sensory nerves in your cornea to the muscles of your eyelid without bothering with the brain. Protecting your eye against something flying into it is a smart thing to do, but it is pre-programmed, it is not intelligence. By contrast, learning that you put the brakes on your car if you see a traffic light turning red is intelligent. You have learned that. If on another world a green light meant ‘stop!’ then your behaviour there would be quite different.

Note that no-where in this have we mentioned language, or technology. These specifically human characteristics we will discuss in the next chapter. Here we are thinking about intelligence rather more broadly.

10.2 Detecting Intelligence

One of the most taxing tasks for a teacher is to detect genuine intelligence in her or his students, and the same applies for testing animals for intelligence. In nature intelligence is detected by observing complex adaptive behaviour in the species’ environment, in particular altering behaviour to anticipate the future, or performing complex activities that need planning, such as a coordinated hunt, which are not pre-programmed. How do we know they are not pre-programmed? That is a major part of the problem. In a laboratory setting intelligence is often tested by exposing an organism to an artificial environment and evaluating its ability to learn complex non-natural behaviour. This is slightly easier, as no animal will be genetically programmed to press levers or run artificial mazes, so solving a laboratory problem is less likely to be the result of instinctive behaviour *if* we design the problem correctly. Common tests include the ability to use tools, generalising from specific experiences, anticipating the behaviour of other animals (in the lab, that other animal is the experimenter). Some such tests have been criticised because they are the sort of test we would do well at. Humans are very vision-centered organisms. We do not use smell or taste much to make plans or understand our world. We are also orientated towards movement. Our very language makes this clear. We say "In the first place, let me say..." and "Oh, I see!", not "Oh, I smell!" or "On the sweet side, I would say...". So tests must be appropriate for the senses of the organism involved.

It seems obvious to us humans that intelligence imparts a selective advantage, and so should be an evolutionary advantage. While the majority of life on Earth remains 'primitive' (from our highly anthropocentric viewpoint), there is a trend that the most complex organisms alive on the planet become more intelligent with evolutionary time. Thus jellyfish show more diverse behavior than sponges, fish show more ability to learn than jellyfish, reptiles show more diverse behaviour than amphibians, and primates are more able to learn complex tasks than any modern insectivore, the group from which primates evolved. But high levels of intelligence are only seen in a few members of each group. Some cephalopods are very smart (we will discuss them below), but most of the molluscs, the larger group of which cephalopods are a part, are literally as unintelligent as shellfish—they *are* shellfish. And the vast majority of the life on Earth is made up of plants and microbes, which entirely lack what we would call intelligence. This is because intelligence comes at a cost. To take in information, process it, remember it and then change your behavior, you need a complex information processing system. For animals, that means a large central nervous system (although *how* large is an interesting question that we will return to later). That costs energy to build, and energy to run. So you need a corresponding benefit to offset the cost. There is no point for a tree to grow an information processing ability comparable to a brain. A brain would enable the tree to anticipate that an elephant or a logger was about to destroy it, but the tree could not do anything about it. Intelligence is useful for some lifestyles, less so for others. So it is not universally valuable.

Intelligence also has a drawback. Pausing to think about something, remember past events, consider the options, might be a really bad idea. That is why your eye-blink reflex does not involve your brain. You need to respond to something approaching your eye in milliseconds, not seconds. Intelligence gets in the way. Many of our actions have to happen too fast for us to think about them. We could not run if at every step we had to think "Ok, now, left or right foot this time?" Flies do not have to think about whether to take off just as your hand comes down to swat them, it is automatic. Pre-programmed responses are faster, and require fewer nerve cells, than flexible, intelligent ones. So intelligence is only useful in some situations.

Nevertheless intelligence can clearly be of advantage. The best example is our species, which through intelligence modified its environment to its needs, colonized nearly any habitable stretch of land on our planet, domesticated fellow animals, and rose to a population of several billion individuals. How likely is intelligence to arise? There are two types of answers to that, the first based on observing intelligent behavior in diverse animals, the second based on working out *how* intelligence happens, what anatomy is needed for intelligence, and looking for the evolutionary traces of that anatomy. Both conclude that intelligence is likely to arise, and its evolution is a Many Paths process.

10.3 Measuring Intelligence

Because there is no universally accepted definition of intelligence, the next practical challenge, how to measure intelligence, is even more controversial. How do you measure something that is only diffusely defined? Science circumvented the problem somewhat by devising different measurement schemes depending on whether individuals of the same species, particularly humans, are compared or different types of species.

There are many tests that measure intelligence of humans, often known rather inaccurately as ‘IQ Tests’. Conventionally, IQ is a numerical measure of general intelligence (called *g*), and is defined so that the average score of a population is 100. High performance in such tests is correlated with academic achievement and career success in Western populations, but it is controversial how far you can use such tests to compare Western populations with non-Western ones. Many tests require knowledge about the European or American world, and even ones that rely on quite abstract ideas, such as Ravens Progressive Matrices (Fig. 10.1), are biased towards people who see simple abstract figures all around them on computer screens, road signs, posters, appliance buttons and so on, and compare them thousands of times a day. People who never see a perfect triangle from one week to the next are at a disadvantage in such tests. The tests also probe specific aspects of intelligence, but what is the most important aspect? Is it memorization? Is it creativity or abstract thought? Is it logic? If a composite of various parameters is chosen, how should it be weighted? So if comparing two humans is hard, how much harder to compare two different species? And this is only comparison. We can easily measure an animal’s weight or height, but an absolute measure of its

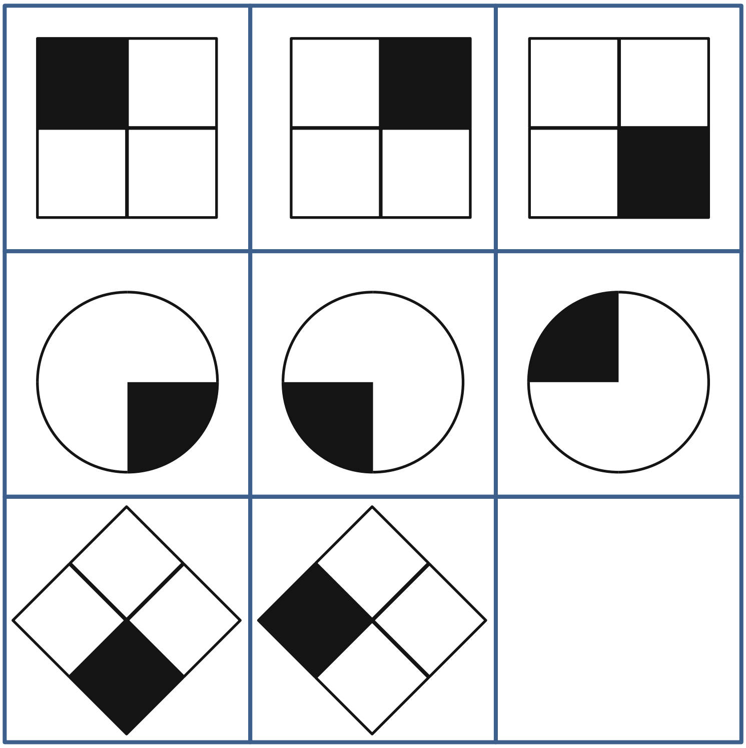

Fig. 10.1 An example of Ravens Progressive Matrices. What should go in the *empty box* on the *lower right corner*? Note that, although this looks like a 'culturally neutral' test of reasoning, it is actually not. People used to looking at a traditional clock face to tell the time will probably find this task easier than people used to looking at digital clocks

intelligence? We don't know how to do it. How would we, for example, weigh the different aspects of intelligence in that species?

So we fall back on looking for specific types of behavior that we think are intelligent, and here we are better equipped.

10.4 Smart Animals and the Distribution of Intelligence

Animals that show intelligence are rather rare considering Earth's total biological endowment. However, they are also spread across different branches of the evolutionary tree, suggesting that intelligence can arise easily if the ecological opportunity to use intelligence arises.

10.4.1 Land Mammals

The most obvious place for humans to look for intelligence is among our nearest neighbours, the primates, which arose from ancestors that lived in forests. Monkeys and apes diverged from other primates about 40 million years ago, and began to evolve larger brains. By about 16 million years ago, apes were distinct from old world monkeys. The apes include two families, the lesser apes and gibbons, and the Hominidae. The Hominidae, also known as the Great Apes, include orangutans, gorillas, chimpanzees, and bonobos, which show an amazing ability to communicate with each other, perceive each other's emotions, and retain lasting memories. Great Apes also show the ability to lie. This might not seem like a major intellectual feat, but it requires several quite sophisticated abilities—the ability to visualize the world as you want it, not as it is (one where I have a banana), the ability to understand what another ape is thinking (that they have seen a banana and want it), and the ability to understand what actions on your part will cause the other ape to have a false view of the world (Oh, there is no banana there after all). And to do all of that while understanding that the other ape may be lying to you as well. This is as complex a cognitive task as trying to learn a new version of Microsoft Windows.

All the Great Apes, as well as gibbons, capuchin monkeys and some other primates, show the ability to use tools. This ability is learned from watching others, it is not pre-programmed. Chimpanzees are most notably skilled at tool use, and they also make simple tools. What is more controversial is whether the Great Apes have culture or language. The idea of ape culture was disputed for many decades, but careful observation in the field now has shown beyond reasonable doubt that chimps, bonobos and capuchin monkeys have sets of behavior that vary between groups and are learned from others in the group. This applies both to practical skills like using tools and purely social acts like how you groom a friend. This is exactly analogous to human cultural differences like whether you wear white or red for a wedding, or drive on the left or the right side of the road.

Animal use of language is more controversial. A few Great Apes have been taught a 'vocabulary' of dozens, in one case over 100, symbols on a keyboard-like arrangement, and have learned to use this to communicate with their human captors. But it is debated whether this is more than learning that pressing specific buttons results in humans behaving in a way they want. Harvard professor Stephen Pinker in particular comments that there is no trace of grammar to their use of symbols. "Koko want banana" and "Banana want Koko" are both used to mean "Koko wants a banana". It is the structure of human language, that way that words play off each other to create new meanings, that is important. Without grammar, a sentence is only a heap of words like this: a grammar heap is like of only sentence this without words. Our view is that there are no animals that show a convincing equivalent of language that comes even close to that of humans.

Several large land mammals other than primates show evidence of intelligence. Elephants, which are related to the cetaceans (whales and dolphins), have the largest brains of all terrestrial animals. Elephants' performance on short-term tests of intelligence, including the ability to learn cause-and-effect, is not that impressive. Where they excel is in learning where things are in space and time, and in remembering and managing very complex social relationships. They can also show surprising sophistication of tool use. Having an elephant paint a picture for you is a common tourist attraction in Thailand; while this may be purely rote behavior, it is very complex rote behavior, and as no two pictures are the same it shows some element of originality. Elephants have also been recorded throwing rocks at animals they want to attack, but cannot reach (specifically, human visitors to zoos). Pigs can learn how to use mirrors to see round corners (some monkeys have been shown to do this too), can work out what other pigs are thinking (Hey, that pig must have worked out where the food stash is), and can 'lie', for example acting to deliberately mislead another pig. Despite what pet-owners the world over believe, dogs are not as intelligent as pigs, although some dogs can learn how to open doors, despite having no hands.

10.4.2 Cetaceans

The order of the cetaceans includes whales, dolphins and porpoises. They probably diverged from the land animals nearly 65 million years ago, becoming amphibious and then entirely marine animals, where the buoyancy of the water allowed them to evolve into the largest animals ever to have lived on Earth. Some of the cetaceans developed very large brains; for example, the brain of the blue whale weighs nearly ten times as much as a human brain. By about 20 million years ago, cetacean brains had achieved essentially their modern size. Most significant is the enlargement of the neocortex, the region of the brain associated with what humans call 'higher' functions—complex reasoning, social interactions and learned tasks (the mechanics of actual memory happen in deeper, more primitive regions). The cetacean's extraordinary reliance on hearing evolved quite rapidly once they changed their living environment from land to entirely marine, as well as other anatomical changes that enabled sound production for echolocation and communication. Cetacean's communication methods are still not well understood. Their vocalizations are quite complex. Cetaceans are good at learning and imitating distinct vocal sounds, and seem to be able to recognize and address each other as individuals. They are also playful and anticipatory. There are many examples of cetacean's highly social and altruistic nature. Based on field studies some scientists even suggested cultural transmission in dolphins.

10.4.3 Birds

Birds show as wide a range of intelligence as mammals, with some being extremely smart. Parrots, cockatoos, and macaws belong to the order of the parrots (Psittaciformes), a group that traces back to a common ancestor about 70 million years ago. Parrots and their relatives have evolved independently on several continents since then. Parrots are known for their high ability to learn complex tasks and manipulate objects in their environment. Some scientists claim they are as intelligent as some non-human primates. Most parrots are very social. The African grey parrot is able to learn several hundred words, in various dialects. It appears that some members of that species can associate words with meaning. Even if this is just clever mimicry (and it probably is), it still shows impressive capabilities of memorization and association.

The gregarious Corvidae, a family of birds consisting of ravens, crows, and jays, are also known for intelligence. Crows have been observed to use automobile traffic to crack open nuts and to use public water dispensers, a behavior they must have learned. The Corvidae display other evidence of causal reasoning, imagination, flexibility, and planning, which is comparable to that of chimpanzees. New Caledonian crows are particularly inventive, and can fashion tools from twigs in the wild or bits of wire in captivity. Recently Hawaiian Crows (living 3800 miles away from New Caledonia across the Pacific Ocean) have also been seen to make and use tools.

10.4.4 Cephalopods

Cephalopods are the squids, octopi and cuttlefish. They are invertebrates, only sharing a common ancestor with the mammals and birds before the Cambrian. However, they too have evolved a remarkable degree of intelligence. Cephalopods became numerous and diverse in the Ordovician time period (Box 1.2), but were mostly wiped out during the mass extinction at the end of the Permian 250 million years ago, with only the octopi, squids, cuttlefish and a nautiloid surviving until today. The survivors were active foragers on the sea floor, which developed acute and sophisticated sense of sight and touch, and very complex nervous systems to control their 8–10 tentacles and their unique jet-propulsion movement. All this required the evolution of substantial intelligence. Although not socially complex, cephalopods' scores in intelligence tests often rival with those of vertebrate animals. They have been observed in the wild to use objects as tools, and in captivity are notorious for being able to work out how to escape from their tanks. They also learn very fast. Researchers putting the common octopus through tests, such as finding their way around the type of maze usually used to test rats or mice, find that the octopuses score very poorly. They solve the problem much faster than rats, and then apparently get bored and stop 'playing along'. While the rats are still learning, octopi have stopped trying. We also are not sure we understand what 'intelligence' means for a creature so different from ourselves, and will probably find even more ways that cephalopods are intelligent as we learn more about what their type of intelligence is.

So intelligence has evolved several times among large, complex animals (Fig. 10.2). All of these large animals have in common that they have significant brains. Thus, the question arises whether it is possible to evolve complex, problem-solving intelligence without a big brain? The social insects provide an interesting case study.

10.5 Social Insects: A Different Approach to Intelligence?

Many insects live in tightly coordinated social groups, with different members of a complex society performing specific functions. Termites, and some ants and bees form complex societies. The feats that social insects can accomplish are impressive. For example, ants are able to cultivate fungi and enslave other species through the use of powerful chemicals, such as keeping termites in captivity in a way analogous to how we keep cattle or chickens. Bees communicate with each other, accurately pointing toward the direction of a good food source. In the bee dance the transmitted information is encoded, which then has to be translated by the receivers—this is not just showing another bee where the food is, it is describing where it is. Termites are able to transform their environment and build structures that are as large in proportion to the

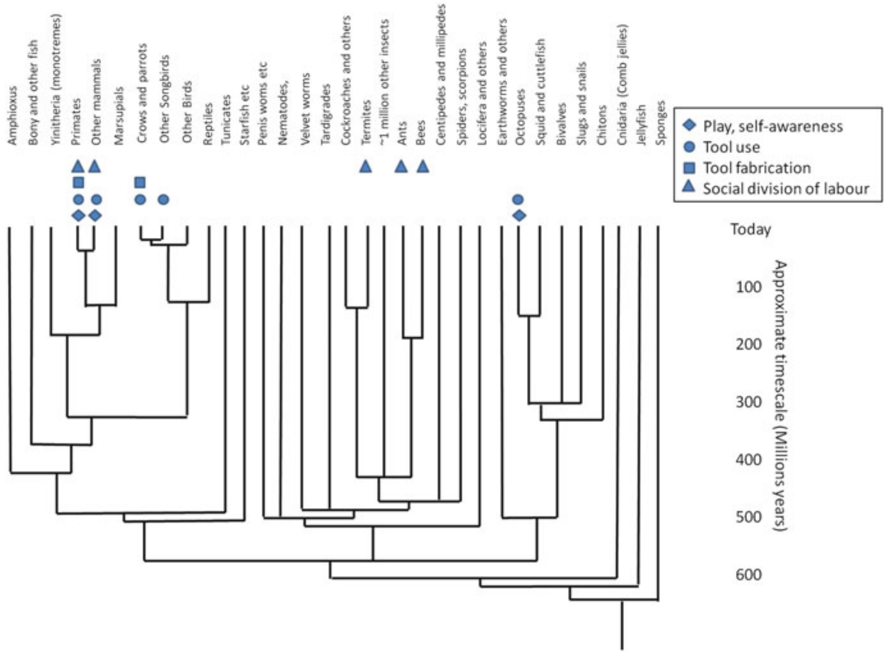

Fig. 10.2 Intelligence on the tree of animal life. Note that this figure is a simplified tree of animal life, collecting many branches that do not lead to intelligent life into single branches—thus the insects, a vast and diverse group of animals, are collected into one branch to make the tree readable. Extinct groups are not included. Branches are labelled according to whether that group of organisms contains animals that use tools, make tools, show other complex behaviour (such as play or self-recognition), or show complex division of labour in social groups

termite's size as skyscrapers are to humans, and also build in passive airflow equivalent to air conditioning.

Nearly all social insects—the ants, wasps, and bees—are restricted to the Order Hymenoptera. While insects evolved in the Ordovician time period from a group of crustaceans about 400 million years ago, the social insects first appeared on Earth at about 150 million years ago. Ants evolved from wasp-like ancestors in the Cretaceous period, about 99 million years ago and diversified after the rise of flowering plants. The commonality between the social insects is the amazingly organized social structure; this "eusociality" has arisen independently in numerous lineages among this group, between 8 and 11 times, and except for the termites, in no other insect order.

The frequent occurence of eusociality in the Hymenoptera has been attributed to the evolution of a sex determination system, whereby one sex has one set of chromosomes (is haploid) and the other has two sets (is diploid). The haploid forms are workers in almost all cases. Because their diploid relatives carry copies of all of the workers' genes, it makes evolutionary sense for the workers to sacrifice themselves entirely to helping the diploid breeders to breed. This means that an animal can become completely specialized to one role—for example that of worker or soldier—to such an extent that they cannot breed, but can still pass all their genes on to the next generation. This includes specialized roles or castes with very specialized, complex behavior.

But is this intelligence? We argue that it is a step along the path to intelligence, but not yet the same as the intelligence we described in octopi or chimpanzees previously. While honeybees can communicate precise information about direction and distance, their communication system is highly stylized and apparently quite literal. They cannot communicate anything other than the distance and direction of food (for example, whether other insects are there eating it, so flying faster would be a good idea), nor the direction of anything else, such as the Bee-Eater bird. Thus, the behavior of individuals shows little evidence of the plasticity normally associated with intelligent behavior.

Both social and solitary insects can show learning. Honey bees have been studied most extensively. Particularly, Martin Giurfa from the Freie University of Berlin, Germany, broke new ground when he showed that honey bees not only display elemental forms of learning, in which bees learn specific and univocal links between events in their environment, but also master different forms of non-elemental learning, including categorization, contextual learning and rule generalization, both in tasks relating to vision and to smell. Most intriguing, when bees were required to respond to a different stimulus; they were able to transfer the learned rules to new stimuli of the same or a different sensory modality. Thus, they show some ability to generalize. This is not just associating one stimulus with one response. However, this is not a complex response, and very simple organism, such as flatworms, can do this to some extent. Flatworms can be 'trained' to associate a light signal with food or with a poison (they move towards it or away from it, respectively). Such generalization is a basic feature of networks of neurons hooked up together, as artificial intelligence researchers discovered in the 1950s.

Bees, termites and ants are not intelligent on an individual basis, but they are so tightly integrated into their society that several authors compared the relationship of the individual insect to the collective not as we might view our membership of our society, but more like the way one cell is incorporated into a multicellular organism. They are totally dependent on the society they are in, and shaped to fulfill its needs. So maybe we are looking at the wrong thing when we ask whether a termite is intelligent. That is like asking whether one of our brain cells is intelligent. We should rather ask whether the termite colony or the beehive is intelligent.

This is a difficult question to answer. If testing octopi for intelligence is difficult, imaging the problems to detecting intelligence in something whose ‘senses’ are the interactions of 10,000 termites running over the surrounding landscape. It is tempting to say that they are, because constructions such as a termite mound (Fig. 10.3) or a bees’ nest is so wonderfully adapted to its environment. But such construction is entirely instinctive. It is like your eye-blink reflex, a marvelous coordination of many different movements and actions, but a pre-programmed response. The social structure of the colony allows for much more complex construction than could be done by one ant or termite on their own. The information processing that guides the construction of a bees’ or ant nest is distributed among the bees or ants just as the computation necessary to blink your eye occurs in an arc of neurons, not one cell. But it is not the result of information processing that looks at a landscape (whatever “looks” means in this context) and designs a better mound. Termites put in Wales would not build a mound with less air conditioning (which is not needed) and more waterproofing (which most

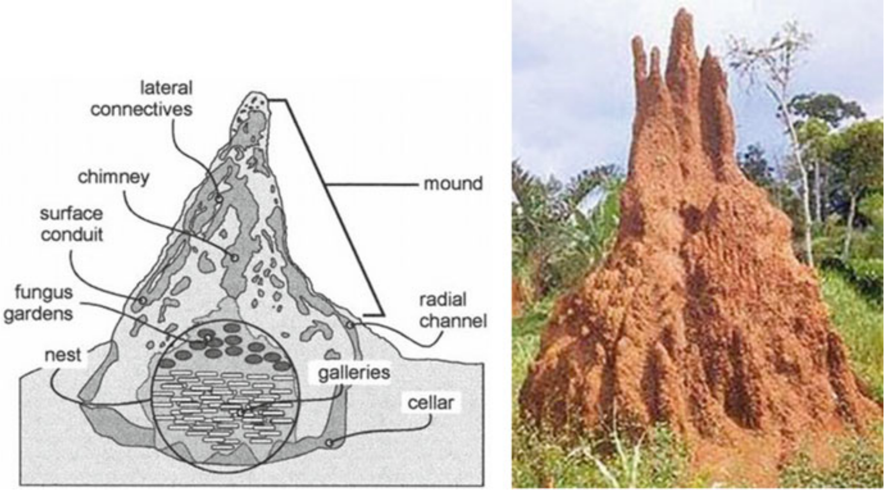

Fig. 10.3 Termite hill, schematic and in nature (Credit unknown, included by courtesy of Mount Moreland Conservancy)

certainly would be needed). They would just build what they usually build in Africa, and as a result almost certainly die. Only mutations in the genes that code for their behavior, leading them to build a different mound, would allow them to survive, and that is not intelligence. That is evolution.

Comparison of termite-mound building to human construction is therefore probably invalid. A better analogy is, again, with our cells. Our cells build the astonishing structure of our hands, a mechanical wonder of bone and muscle and tendon and cartilage, which seems uniquely well adapted to holding stone axes, playing the flute or typing books. But if the world was flooded our cells would not 'decide' to grow flippers instead. We would continue to grow hands until mutations changed the program.

Do colonies of ants or bees solve problems, have a collective memory, make extrapolations, use generalizations, other than through passive reaction to the world? We do not know. There are some behaviours that look intelligent. Ants foraging for food will quickly set up a trail that is the shortest route from the food to the nest. Surely this takes planning? But in fact this is just each ant following a scent trail and occasionally wandering off it. If by accident it discovers a short-cut, then there are two trails, and the shorter one gets preferred because the scent the ants leave behind does not have so much time to fade on that one. This is smarter behavior than any one ant can manage, but is still pre-programmed.

So social insects do show 'swarm intelligence' (also sometimes incorrectly called 'meta-intelligence), in that the behavior of the whole colony or swarm is more complex than the behavior of any individual, and more complex than the behavior that any individual could perform, with its tiny brain. Such swarm intelligence is not confined to the insects. The instantaneous changes in direction of a whole flock of birds or shoal of fish shows the same sort of distributed decision making between many individuals, although nothing like the complex behavior that leads to a 3 m high termite mound. But it has not yet made the jump to the sort of intelligence that allows a crow to bend a piece of wire—a material it has never seen in its life before—to fish food out of a tube, or that leads an octopus to "think" that an abandoned tin can is an artificial protecting shell.

10.6 Mirror Play

There are two other attributes that do not directly show intelligence, but are strongly associated with it. These are self-consciousness, and play.

If intelligence is hard to define and detect, self-consciousness is almost impossible. Even in humans, how can you tell that someone has a sense of self? I can program my computer to say "I feel really tired", but that does not mean that the computer is self-conscious. Logically, the same should be true of people. If someone says to you "I am bored, I want to go home", we suppose that they have a sense of self, an internal model of their own existence which is, at that moment, bored. But is that true? Or is what they are saying a reflex, like an eye-blink, more sophisticated to be sure, but basically a set of complicated but entirely predictable reactions to (for example) listening to political speeches? By convention we assume that other people have a sense of self, because we assume that if other people behave like us, then their internal life is like ours. I am aware, so I assume William is too. But maybe he is just a robot? In fact, the whole behaviourist school of psychology was based on saying that statements about what 'I' felt inside my head are meaningless, and what we should focus on is an animal's actual behavior.

Luckily, there is a test based on behaviour invented by psychologist Gordon Gallup Jr. in 1970, called the mirror test. It is not that reliable, and there is fierce debate about what it means, but the essence is this. You put a harmless mark, maybe a chalk dot, on an animal in a place where they cannot see it. You show by watching their behavior that they do not feel you put it there. Then you show them a mirror. Do they realize that the thing they see in a mirror is not another animal, but is in fact "Me"? And "Me" has a dot on "my" forehead? If they explore the mirror, and then start to explore their own head to find the mark, they have made the connection between themselves and the image they are seeing. They do not know how, but the mirror shows "Me".

It is accepted that humans pass the mirror test, as do chimps, bonobos, orangutans, elephants, dolphins, orca, and Eurasian magpies. Interesting, gorillas cannot reliably pass the test, and one parrot species tested also failed, as does the octopus. But the test is not ideal. It relies on an observer's interpretation of an animal's actions. The test also depends not only on the animal using sight as a major way to study the world, but also being used to looking at other animals. For a gorilla, looking directly at another gorilla is an aggressive, threatening act. They may just never look at the "other" gorilla in the mirror long enough to realize that it is in fact them. Even young humans can fail to pass the test if brought up in a culture without access to mirrors. So this is by no means a good test. But in the absence of mind-reading machines, it is the best we have, and it confirms at least that self-awareness is an aspect of mental life that has evolved independently in several evolutionary lines.

The other behaviour that is associated with intelligence is play. The young of many animals play, and generally the smarter they are the more they play.

Humans are an extreme example, with adults in Western society spending most of their waking hours in activities not obviously related to survival (gaming, watching TV, playing golf, reading books like this one). Like 'intelligence' and 'self-awareness', 'play' is very hard to define. Play researcher R. Fagan defines play as "improvised performance, with variations, of skilled motor and communicative actions in a context separate from the environment in which behaviour including these actions proximately increases reproductive success." In other words, play is doing things you would normally do, but not when and how you would normally do them. Cat's stalk and pounce on leaves (rather than prey), dogs chase their tails (rather than deer), horses jump and 'frolic' (rather than run from predators). There are many theories on why animals play, but one accepted by many (including us) is the 'Instinct Practice' theory. This theory says that play is to hone behaviours, practice complicated instinctive actions, and teaches the animal the limits of its own abilities. Play is seen as a way of practicing for adult life. But why would you need to practice? A worker bee does not need to practice the Wiggle Dance—it is programmed in, ready to use. We do not need to practice breathing—it just works on its own. What we practice is the complex behaviours that are *not* pre-programmed—things like getting along with each other, coordinating hunting, finding a mate. The more these activities are left to our intelligent minds—although the basics are pre-programmed—the more the specific details are left to us to work out. The more they are not pre-programmed but are flexible, the more we need to practice them before we get to try them out in the real world.

And the most playful animals indeed are the ones that score highest on other scores of intelligence. They are the primates, the cetaceans, and elephants. Seals and their kin, and carnivores like wolves, bears and big cats are also notably playful.

It is hard to know if a cephalopod is being playful. If play is repeating actions out of their usual, functional setting, how do you tell if an animal with no bones is repeating an action? But octopi seem to 'play' with things in their environment, including things that could not possibly be food, a threat or a mate, like Lego blocks. They also have a wicked sense of humour when it comes to dousing their keepers with water.

So direct tests of intelligence, and tests for associated mental states like self-awareness and play, show that intelligence has arisen in at least six groups of animals. Even if we discount the social insects, we find intelligence in the primates, several other mammal groups such as the Afrothera (elephants) and Artiodactyles (pigs), the Passeriformes (birds like crows and parrots), the Cetaceans and the Cephalopods.

10.7 Where Does Intelligence Help?

We see intelligence in diverse species, but not in all species. So what lifestyles encourage the evolution of intelligence?

There is no very clear pattern what animals evolve enhanced intelligence. Primates are mostly highly social, but Orangutans are an exception, and octopi are quite solitary animals. Most animals with high intelligence hunt (mostly as part of an omnivorous diet), and it makes sense that you have to be intelligent to outsmart other animals. But elephants and gorillas are herbivores. There seems to be little common factor. This supports the Many Paths hypothesis for the evolution of intelligence. It can arise as a result of many different ecological demands, not just one, unique set of circumstances. Elephants have to be smart to manage their complex social structure and remember the huge landscapes over which they roam. Primates have to be intelligent to manage social structure and coordinate hunting and food gathering. Crows need intelligence to gather enough food to keep their high energy metabolism going on small islands like the New Caledonian Islands, where food is scarce. And maybe octopi need to be smart just to control all those tentacles.

Intelligence has arisen in very different time periods and in distantly related clades of life. For example, the first octopi evolved probably between 500 and 450 million years ago, while the first brainy dolphins appeared about 20 million years ago and the first humans probably 5 million years ago. First octopi, and then whales, dolphins, and porpoises were the smartest animals on our planet for a long time. The different organisms that exhibit exceptional intelligence, only a selected few of the many species of Earth's biosphere, are only distantly related to each other. For example, the octopus from the invertebrates is so distantly related to the vertebrates that their brains show little resemblance to each other. Also, there does not seem to be a single ecological theme that ties the groups of the more intelligent species together. Marine, terrestrial, and even arboreal flying habitats are all represented. However, there appear to be some factors that enhance the chances for developing intelligence, which are summarized in Table 10.1.

These factors suggest that intelligence is selected in some lifestyles and not others, and this fits with where we see intelligence in different organisms. It might seem obvious for us humans that intelligence is a selective advantage for any animal, because intelligence was the basic requirement for us to become the dominant species on our planet. However, biology does not support this conjecture. Yes, intelligence is common, but only in a minority of organisms

Table 10.1 Some factors promoting the evolution of intelligence

Promoter	Reasoning	Example
Body size	Intelligent animals tend to have larger body sizes compared to the average of their taxonomic group	Cephalopods, elephants, social insects[a]
Active lifestyle	A high degree of sensor processing and motor control, particularly in regard to acceleration and balance, depth perception, feature extraction, distinguishing foreground from background, spatial orientation, memory, and coordination of muscle activity are needed for an active lifestyle	Dolphins, humans
High sensory resolution	High intelligence goes hand in hand with sophisticated sensory processing. Examples are the hearing and echo-locating abilities of marine mammals and life in complex arboreal habitats	Primates, parrots, cetaceans
Fine motor control	Combination of delicate and complex movements including the coordination of multiple appendices and subtle muscle movement to control vocalization. An example is again the arboreal lifestyle, which puts a premium on eye-hand coordination, depth perception, and acuity	Octopus, parrots, human
Social behavior	Intelligence is needed for detailed communication either by vocalization, facial expression, or behaviour. It often includes hierarchical and territorial awareness, and accurate social memory	Primates, cetaceans, social insects[a]

Modified from Irwin and Schulze-Makuch (2011)

[a] Social intelligence, not individual intelligence

within a certain clade, and most of the biosphere, particularly microbes and plants are rather non-intelligent.

There is one other factor we did not include in Table 10.1, but which may be one of the most important ones, so we discuss it below in detail. In general, predators are smarter than their prey. Prey such as cows or gazelles only have to have intelligence enough to recognize a predator, coupled with strength to fend off that predator or speed to run away. Thus, the selective advantage is body mass or strength, and speed, together with acute senses and the intelligence to use them to detect the slightest hint of threat. For the predators, as well as the complex sensory information to find the prey, they have to anticipate the reaction of the prey to being attacked. The selective advantage of the lion is based on both body strength to bring the prey down and on intelligence to catch it in the first place. The situation is even more challenging for wolves, which hunt in packs. Pack hunting requires communication and coordination with other wolves as well anticipation of the hunt to be successful. Thus, it would seem that the greatest selective advantage of intelligence would be for a social predator. This reasoning does fit for us humans, and also for dolphins, but fails for octopi.

There are a variety of other strategies to achieve the same goal, however. Depending on the strategy used, intelligence is needed or not. Think about a snake that is well-camouflaged waiting simply for a frog to hop by. The selective advantage is the camouflage and the quick reaction to catch the prey, including the ability of secure grip with strong teeth or the use of venom to prevent the frog to escape. Using such an approach, intelligence does not seem to make much of a difference.

Animals that have to range widely for food also tend to show higher intelligence. Ruminants like cows and goats eat anything green, and so do not have to remember where the last meal was. Other animals like bears (large animals living in relatively food-poor environments), or great apes (fruit-eaters, who have to range across a wide territory to find their specialist foods) may have to remember where food was this time last year, not just where they found it yesterday. So we would expect intelligent animals to be ones with wider ranges. If they travel in large social groups this adds to the complexity, as 50 chimps need a larger range to feed over than just one (and they must remember who is who in the group as well).

Thus, intelligence seems to be a selective advantage for some animals in some situations and habitats, but not for others. Intelligence has a cost as well as an advantage. Large numbers of complex nerve cells require energy to build and maintain. And intelligence can be a drawback. Instinctive reflexes are much faster and generally more reliable. The cost of intelligence must be counterbalanced by a need for flexible, general problem solving abilities, and it seems this balance is less often in the favour of smart animals than we, self-styled “Man the Thinker” (Homo sapiens) might want to believe.

The review above does however suggest that intelligence has evolved many times in different clades, and from different bases. But one common theme is that all intelligent animals are... animals. They all have a common origin around 550–600 million years ago. Maybe then intelligence is an unusual side-effect of animal anatomy on Earth, and would not evolve elsewhere? We think not, because when you look at how intelligence has evolved it has evolved through different paths as well as different lineages. This brings us to the discussion of brains.

10.8 Building Intelligence

Humans have comparatively huge brains. Humans are smart. Generations of scientists have therefore assumed that humans are smart because we have disproportionately huge brains, and consequently any animal with a big brain will be smart. However, while it is clear that a complex nervous system is needed for complex behaviour, the relationship between brains and intelligence is not as simple as it appears.

Complex adaptive behaviour is not the prerogative of organisms with nervous systems. The unlikely candidate is a slime mold, *Physarum polycephalum*, which translates as "the many headed slime" and which reminds one of the TV cartoon character *Patrick*, the starfish from the TV show SpongeBob Squarepants (Fig. 10.4). The slime mold prefers to live in damp, shady areas, especially decaying logs and leaves, and is sensitive to too much light. This gelatinous representative of the Amoebozoa phylum behaves sometimes like a colony of cooperative individuals foraging together and at other times like a single cell containing millions of nuclei. *Physarum polycephalum* is highly optimized in shape-shifting and moves from one place to the other by a process called shuttle streaming. In shuttle streaming the protoplasma of the slime mold is moving rhythmically to and fro, with the force being generated

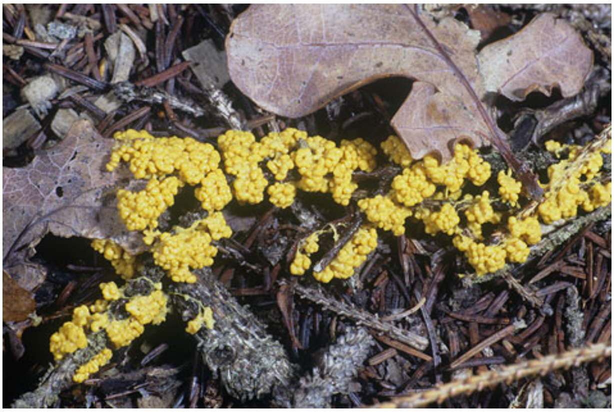

Fig. 10.4 Plasmodial Slime Mold (*Physarum polycephalum*) growing on litter on the forest floor. Credit: George Loun/Getty Images

by a pressure gradient from the contraction and relaxation of a membranous layer, not much unlike how our muscles work.

The shape-shifting ability of the slime mold comes handy for solving the so-called Shortest Path problem. Toshiyuki Nakagaki from the Bio-Mimetic Control Research Center in Japan and his colleagues cut up small pieces of the slime mold and put these in a maze. The plasmodial pieces spread and coalesced to form a single organism that filled the maze, but more than that happened. When grown in a maze with oatmeal at two locations, *P. polycephalum* retreated from everywhere in the maze, except the shortest route connecting the two food sources. When the slime mold was offered more than two food sources, a more complicated network pattern was the result. In fact, when Nakagaki and colleagues dispersed oatflakes to resemble Tokyo and 36 surrounding towns, *P. polycephalum* formed networks with comparable efficiency, fault tolerance, and cost comparable to the Tokyo rail system. Since *P. polycephalum* was also shown to mimic highway systems in Canada, the U.K., and Spain, the researchers suggested that the networks produced by the slime mold may be used as a model to design real-world infrastructure networks.

Physarium polycephalum has also some other amazing abilities in information storage ("memory"). In another experiment, when the slime mold was subjected to unfavorably dry humidity conditions once every hour, the mold started to anticipate the dryer air and moved more slowly even if the humidity was not lowered anymore. If the dry periods were not further applied at the regular intervals, the slime mold's "sense of anticipation" gradually faded away. However, when only a singular dry pulse was applied 6 hours later, *P. polycephalum* returned back to the earlier rhythm. Whether this kind of adaptive behavior can be labelled learning is questionable, but it shows that the amoeba-like organism has a cellular memory.

Is this behavior 'intelligent'? It is certainly complex and adaptive, but the mould has no ability to generalize from one problem to another, and no ability to learn other than the simple cellular memory described above. What is key is that these abilities reside in the aggregate slime, not in individual cells. It is cells communicating with each other, each processing a tiny fragment of information and passing it on, which results in complex behavior. The roots of all complex behavior lie in cellular communication. Molecular genetic studies suggest that the molecules used for cells to communicate with each other evolved long before life developed the complex behavior that relies on those molecules, and evolved separately many times in bacteria, archaea and eukaryotes.

In eukaryotes, however, cellular communication could be developed beyond anything that single celled organisms can achieve, through two processes. Firstly, it could be speeded up, by replacing slow chemical processes for fast electrical ones. Secondly, specialist cells that do nothing but transfer and process electrochemical signals can evolve. In animals these are the nerve cells that make up the nervous systems of all animals, from nematodes to humans. Organs whose function is processing information and which rely on nerve cells can then evolve, and the result is brains.

There is no clear single point in the evolutionary tree of animals where complex brains appear, and according to Leonid Moroz of the University of Gainesville, Florida, central nervous systems evolved independently no less than five times in molluscs alone. A 'brain', i.e. an organ devoted to information processing, probably evolved several times from simple neural networks. Nervous systems were already well-developed by the Cambrian time period, about 541–485 million years ago, according to Nicholas Strausfeld from the University of Arizona, who analysed several fossil arthropods. There are traces of a central nervous system in 520 million years old shrimplike fossils, which are interpreted to be complete three-part brains, similarly to many arthropods today which exhibit the rudimentary basic structure of our brains. With complex nervous systems in place in the Cambrian, it is likely that basic neural nets were present in the Precambrian Ediacaran animals, dating back to 600 million years ago.

So nerves and simple brains evolved several times, and the acquisition of a nervous systems capable of taking in sensory inputs, processing them, recording inputs and actions, and directing an animal's behaviour is a Many Paths process. This is underlined by the finding that plants can also have fast signalling pathways between different parts of the organism. Plants do not have nerve cells as such. But they do have electrochemical pathways that communicate quickly around an organism, and some can respond rapidly to distant stimuli as a result. The most spectacular examples are carnivorous plants like the Venus flytrap, where a touch on a single hair causes the whole trap to close fast enough to capture an insect. Pitcher plants and mimosa also show movement fast enough for humans to see (and mimosa's movement can be blocked by anaesthetics, just like ours). Part of the flower of Trigger Plants (called the "Floral Column") responds to a slight touch by snapping forward to cover a wandering insect in pollen. The carnivorous bladderwort traps microscopic insects in an open sack: when the insect swims in, the trap shuts in under 10 milliseconds, requiring coordinated movement at least as sophisticated as your eye-blink. In many plants the chemical mechanisms that communicate signals rapidly between different parts of the plant work in a way that are quite similar in principle to how our nerves work, although they evolved quite independently. Of course, plants never evolved even the most basic form of intelligence. But they show that the first step to intelligence, the development of a fast communication system to link sensing and movement, can and has evolved many times.

Once we get beyond the possession of nerves, the requirements for the evolution of intelligence become murkier. In vertebrates, generally the larger you are the bigger brain you have, but this does not mean that big animals are smarter (women, who on average have slightly smaller brains than men simply because on average their whole bodies are slightly smaller, have been saying this for decades). Larger bodies seem to need larger brains, just as they need larger guts. If we plot the brain and body weights of mammals on a graph (Fig. 10.5), we see a clear trend. A few animals break the trend, and the smarter they are the more they break it. Thus, humans lie well above the line of the average for mammals, as do dolphins, chimpanzees and other smart animals. This suggests that it is not brain size *per se* that is important for intelligence, but larger brain size than expected for a body of a particular size.

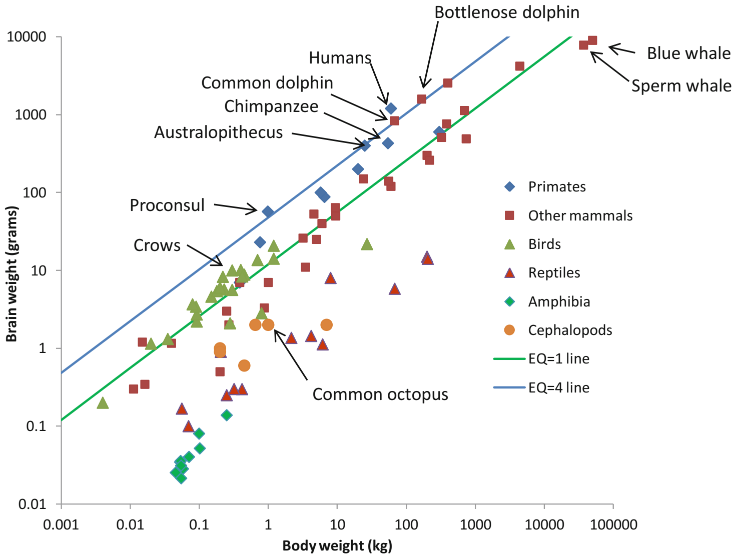

Fig. 10.5 Adult brain and body weight for selected species. Also shown is the *line* for EQ = 1 (the average ratio of brain: body for mammals) and EQ = 4 (roughly the highest brain: body ratio seen, other than in humans). Note that, although each species is shown as a single point, in reality their brain and body masses vary significantly between individuals

To measure this, zoologists have developed the idea of the Encephalization Quotient. The formula for EQ mammals is

$$EQ = \frac{R}{0.12 \cdot B^{\frac{2}{3}}}$$

where EQ is the Encephalization Quotient, R is the brain mass (in grams), and B is the body mass in grams. The numbers 0.12 and $^2/_3$ are just found experimentally to be so for mammals, there is no theory predicting them, a problem we will come to below.

The 'average' EQ for a mammal is 1, and as expected, smarter animals have higher EQs, with humans being on top of the list (Fig. 10.5).

However, even among mammals this is not a perfect predictor. The Blue Whale has quite a low EQ, despite being recognized as at least as smart as dogs or cats (Table 10.2). This is likely due to its enormous extra weight in fat tissue, which the EQ approach does not correct for sufficiently. Also, experience shows that computed EQs show quite a bit of variety depending on the scientist doing the analysis.

Nevertheless, some relationship between more closely related animals can be observed. First, the EQ of predator species is generally higher than that of animals preyed on. Prey species that use active predator avoidance strategies have a higher EQ than that do not use avoidance strategies. The EQ of species that have social interactions is generally higher than those that do not or only have very little. All of this matches with the behaviours that, as we noted above, tend to be correlated with observed intelligence.

However, when we look at animals other than mammals, the relationship of EQ and intelligence starts to break down. Birds generally have much lower EQs than mammals, and even the smartest of birds, the crows and parrots, have only average EQs. This is paradoxical, as we would not expect flying species like birds to carry excess fat like Blue Whales. A solution to this might be that bird's brains are structured differently from mammalian brains, with more nerve cells and fewer supporting cells. Pavel Němec at Charles University in Prague measured the numbers of nerve cells in brains of many animals, and found birds often had far more nerve cells per gram of brain than mammals, especially in the critical regions of the brain often associated with complex thought. For example, the raven's brain had more nerve cells than the capuchin monkey, a primate whose brain weights four times as much.

EQ breaks down completely when considering the cephalopods. Cephalopods such as octopi have a brain which is quite small compared to a human brain. Instead, two-thirds of an octopus's neurons are found in the nerve codes

Table 10.2 Encephalization quotients (EQ) for selected species

Species	Body mass (kilogram)	Brain mass (gram)	EQ
Human	61	1400	7.50
Bottlenose dolphin	167	1587	4.35
Australopithecus	25	400	3.90
Gibbon	5.7	100	2.60
Chimpanzee	54	430	2.50
Baboon	20	200	2.26
Rhesus monkey	6.5	88	2.10
Crow	0.3	10	1.86
Gorilla	128	550	1.80
Fox	4.6	53	1.60
Jackdaw	0.2	6.023	1.47
African elephant	4420	4200	1.30
Rook	0.42	8.358	1.24
Horse	324	510	0.90
Mole	0.0396	1.16	0.83
Sheep	55.6	140	0.80
Lion	200	300	0.73
Blue whale	50000	9000	0.55
Mouse	0.01118034	0.3	0.50
Hedgehog	0.877	3.3	0.30
Loligo (Squid)	0.2	1	0.24
Goldfish	0.0055	0.069	0.18
Octopus vulgaris	1	2	0.17
Thresher shark	70	31	0.15
Barracuda	4.79	4.34	0.13
Garden lizard	0.056	0.168	0.10
Turtle	2.163	1.36	0.07
Iguana	4.19	1.44	0.05
Mississippi alligator	205	14.08	0.03

of its tentacles. Thus, they do have highly complex nervous systems, but not all is concentrated in a central processing unit, but rather is distributed throughout the body. So we would not expect them to have big brains. Nevertheless, they have clearly shown intelligent behavior on many occasions. If we count all the nerve cells in their body, and compare this with mammalian or bird brains, does this explain their intelligence? *Octopus vulgaris*, one of the smartest of the cephalopods that shows learning, problem solving, playing and tool use, has the same number of neurons in its entire nervous system as an owl monkey, and three times as many as an opossum (a mammal of similar weight to an adult octopus). So again, perhaps it is number of nerve cells that is most important, rather than anatomy or mass of the organ that they are in.

These differences suggest at least three different ways that a nervous system can develop sufficient complexity to show intelligence. The mammalian way is to expand the whole brain. The bird way is to expand the number of neurons in a central brain. Cephalopods expand the total number of neurons, centralizing some in a brain-like organ but leaving most distributed across the body.

So exceptional intelligence in the natural history of Earth seems to go hand in hand with developing organs that provide a large number of nerve cells, but enhanced cognitive capacity emerged from different starting points in the more intelligent species. The driver of intelligence appears to be related to the need of more nerve-based processing power such as complex motor skills (in the octopus) or complex social and communication needs (in the cetaceans) or both (in the primates). Given that intelligent species arose many times in vastly distantly related organisms and very different time periods, it can be concluded that intelligence will arise as normal consequence when an elaborate food chain has evolved that includes predators, prey, and omnivores. It is thus a Many Paths process and it can be expected that it will also occur on alien worlds.

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11

Technologically Advanced Intelligence

In the last chapter we pointed out that many different groups of animals have evolved the ability to use tools, solve problems, plan ahead, and learn complex behaviour. But there was one species whose ability to do this is so extraordinary that it belongs in a class of its own. That species is, of course, our own: *Homo sapiens*.

What humans do goes beyond just using objects in their environment as tools, or fashioning tools by bending, splitting or breaking twigs or leaves as other animal species do. Humans have built a technological material culture in which devices of extraordinary complexity are made from materials from hundreds of sources and the learned input of tens of thousands of people. Ordinary, every-day objects like a sheet of paper or a roll of adhesive tape are the output of an industrial complex that spans continents, and could never be made by one person in the forest in Gombe, or for that matter a group of people in any place or time before about 3000 BC (try to make paper yourself from bits of wood, without buying any chemicals at your local store. Never mind making something good enough to feed though your printer. Just try making it flat enough to write on). Although the roots of our intelligence lie in our evolutionary past, something about humans is different. That something is called Technology.

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11.1 What Is Technologically Advanced Intelligence?

We understand technology to be something more than tool use, which as we saw in Chap. 10 is relatively common in a wide variety of animals. Human technology differs from these examples in extent and in kind. Our technology is designed and learnt (rather than instinctive), is specialized (so that some humans do nothing but make artefacts for others to use), and often harnesses external power. Technology links many different tools and behaviours into an integrated whole, whether it is a subsistence level farm or a space station. It is also passed on by explicit teaching from generation to generation, a task that in theory does not require language but in practice uses it extensively. Only the human species *Homo sapiens sapiens* achieved significant technology capabilities on Earth. Was this a uniquely unlikely event?

There certainly were other human species that were able to manufacture tools and use them in broad contexts such as *Homo ergaster*, *Homo habilis*, and *Homo erectus*, with some members of the Homo species likely being able to control fire (e.g., *Homo heidelbergensis* and *Homo neanderthalensis*). But these are closely related to *Homo sapiens*. A point in case is that of the Neanderthals, which could even interbreed with humans that were anatomically indistinguishable from modern humans. All these now-extinct groups of the genus Homo could manufacture tools far more sophisticated than any made by non-human animals today. So all of the genus Homo may have been on a path to a technologically-capable species from over half a million years ago. Were the achievements of the other human species still on the level of tool manufacture and use as observed in other animal species, or did some of them already reach the threshold of what we would call technological intelligence? Would the control of fire be that threshold or perhaps that ability in conjunction with manual dexterity, complexification of social interactions and particularly the development and dependence of a language as seen in *Homo sapiens sapiens*?

We are interested here in advanced technology, by which we mean a suite of techniques and skills and the tools that enable them, including tools that are used only to make other tools, and tools which exploit a non-biological powersource. Examples of such technology are sailing ships, waterwheels, steam engines and the internet. There are many stages on the road from our primate ancestor's skills to this level of advancement.

11.2 The Human Path Toward Technologically Advanced Intelligence

We have seen how tool use is widespread among animals. However, tool making is rare. Australopithecus shows evidence of habitual tool use in the bone structure of the hand. Humans have a powerful grip coupled with precise control of gripping and twisting forces, which are reflected in the internal structure of the bones of our hand. Chimpanzees do not have those structures, *Australopithecus africanus*, which lived between 3.2 and 2 million years ago, had more human-like than ape-like bone construction in this regard, and made flaked stone tools. So by 2 million years ago humans were specialized not just to use tools but to make them. However, it is not clear how critical these features are to taking the first step on the path to complex tool manufacture. In 2016, Tomos Profitt and Michael Haslam observed capuchin monkeys in Brazil breaking open flint stones to produce sharp-edged flakes very similar to the stone tools made by Australopithecus. They did not use the tools—in fact, it was quite mysterious why they were breaking the rocks in the first place. However, the Capuchins clearly had the strength and dexterity to crack rocks to produce what an archaeologist would see as a basic stone tool.

There is some evidence that humans had found out how to use fire 1 million years ago, a key step from total subservience to environmental conditions. Fire provided humans with a concentrated and controllable source of energy. It gave them respite from cold, expanded their diet through cooking, and probably afforded them protection from wild animals. Much later, it would become an important aid to fabrication. But this was not yet technology. It was a tool.

So what distinguishes the tool from the technology? A critical feature is specialization, and its necessary adjunct, exchange. Humans spontaneously exchange things from early infancy. Some animals can be trained to exchange one thing for another in a laboratory setting, but it is almost unknown behavior in the wild. Humans exchange objects all the time. One food stuff for another, an axe for food, an axe for a decorative shell. 100,000 years ago, long before the start of agriculture, we know that modern humans were exchanging materials such as useful rocks or decorative shell over quite long distances. This was trade by any other name. Trade needs some way of communicating what you want. Sign language can work, but it is a language. By contrast, Neanderthals probably did not exchange materials with outside groups. Neanderthal tools are always made from local materials.

Exchange is critical because it lays the bedrock for me, an expert in making stone axes, to focus on what I am good at, and you, an expert in using those axes to kill deer, to focus on what you are good at. I make axes and give some to you, you kill deer and give some to me. We both win. Once I have specialized as an axe-maker, then I am more likely to come up with a better way of making axes. After all, I do it all day. Even chimpanzees, which make and use tools for food gathering, never do this type of specialization-based exchange. At most, an adult chimp will help their own juvenile offspring by selecting or making a tool. The appearance of exchange in the archaeological record closely follows a rapid enlargement of the forebrain (neocortex) about 200,000 years ago. This not only enabled the fine motor control required for tool use and vocalization, but also expanded brain areas for planning and abstract thought. These abilities may also have spurred the development of symbolic spoken language, which facilitated increasingly complex social interactions needed for such trade exchanges to work.

11.3 The Power of Social Structure

Humans are extremely social animals. The famous biologist Edward O. Wilson argued once that we as human beings are really eusocial apes, just as ants are eusocial insects, and that with our brand of extreme "togetherness" we stand apart from other apes, and even from other hominids. Our "togetherness" is certainly not as close as in termites, ants, or bees. Eusociality in these animals, and even in mole rats, an odd-looking and very long-lived eusocial rodent found in East Africa, is associated with cooperative brood care, presence of overlapping generations within a colony of adults, and division of labor into reproductive and non-reproductive groups. All humans are extremely interested in reproduction, and fiercely defend their right to have their own children—as biologist and writer Matt Ridley puts it "Even the English have not given away their rights to reproduce to a queen". However other aspects of our sociality are much more complex than in other primates. Oxford anthropologist Robin Dunbar argues that this is as a direct result of our big brains, and our brains evolved not to work out how to flake flint but how to interact with many other humans. Dunbar has observed that humans typically operate in groups of around 150 people (others have called this 'Dunbar's number', although Dunbar's own research shows the number can vary between 100 and 250). Neolithic villages, basic units of armies from the Romans to the modern day, college fraternities all work best when composed of 100–150 people. Even if you have 5000 Facebook friends, it is almost certain that you will only actually interact meaningfully with 100–200 of them. By contrast, bonobo, chimp and gorilla troops rarely exceed 40–50 individuals. Humans seem to be able to handle a much denser, more complex social network. Perhaps the ability to put yourself inside the mind of a dog or a horse is a spin-off benefit of being able to imagine what 150 other people think of you.

Is this ability the key to our exchange of ideas and objects? It is likely to contribute, but cannot be the whole story. If brain size and social group size are related, as Dunbar argues, then Neanderthals should have at least as large a social circle as we do, as their brains were actually larger than modern humans.

Human social behavior may be much older than once believed. Until recently, we modeled the behavior of the ancestors of apes and humans on the behavior and anatomy of modern apes like chimpanzees and gorillas. Their social structure revolves around the dominant male (and his mate). The males develop large incisor teeth for fighting and to dominate the females. Infanticide is common; when a male gorilla wins a female from a rival, he will often kill the rival's infants so he can replace them with his own. It has long been assumed that the relatively smaller teeth of the bonobo, together with its society dominated less by fighting and more by sex, was derived by evolution from a more aggressive, chimp-like state. Humans were also assumed to have evolved our less fight-orientated anatomy and (by inference) more complex social structures late in our evolution.

The discovery of Ardi (*Ardipithecus ramidus*), a primate clearly belonging to the human lineage dated to be 4.4 million years old, suggests that this story is not correct. Ardi's anatomy indicates that she was a humanoid living in the trees and not in the open savannahs. Ardi, and the remains of about 30 other individuals recovered, show that *Ardipithecus* did not have large canine teeth in males, but that the teeth were the same size between males and females, just like in modern humans. This suggests a more complex social structure, and one less dominated by male aggression and physical threat. Perhaps then the social structure of our common ancestor was a simplified version of human and bonobo structures. The chimps and gorillas went in one direction, early hominids went in another. This has important implications. If I am seeking a mate, then for a chimp or gorilla physical prowess is important. If I am an australopithecine, however, social prowess becomes as important as the size of teeth or muscles—although we must admit that even today physical appearance is a significant factor in mate choice in humans. The fitness of a social animal is not only measured at the physical level anymore, but also by its social skills and its role in the community. A single individual can now have lasting effects on the entire community and not only on its own offspring. This line of thinking is supported by the fact that some social animals show no differentiation between their own offspring and others from members of their group. This kind of community approach is also practiced in the *Canidae* (e.g. wolves), in which the whole community relies on a single reproductive couple for offspring.

So why haven't chimpanzees developed their intelligence further? After all, genetically they are very similar to us humans and they do have a complex social structure including communal learning. Males are selected on their ability to be socially dominant, which is practiced by force, intimidation, projecting a fear atmosphere and constant aggressive displays. There is a constant threat that the young are being killed. Although chimpanzees do develop life-long bonds with other individuals, the cohesion of the group is weaker compared to the *Canidae*. Chimps have more episodes of in-group violence with a higher severity of violence, demonstrate less group bonding and sacrifice for their group members, and invest very little (if at all) in the offspring from others in the group. In such a social environment, investment in learning and the community pays off to a much lesser degree. In humans, social dominance has a much greater role in mate attraction. As Henry Kissinger, former U.S. Secretary of State under the presidents Richard Nixon and Gerald Ford, said, "Power is the ultimate aphrodisiac". Henry Kissinger was 1.75 meter tall, slightly chubby, had bad eyesight, but was sought after by women because he had social power, not physical power.

11.4 The Final Steps to Technology

The next critical step on the road toward technology was probably the domestication of wild animals—especially dogs and several hoofed animals. It is likely that dogs were the first to be domesticated, and they at least in part domesticated themselves. A wolf pack would learn to hang around the human 'pack', because humans with their spears and stone tools could bring down big, dangerous game, and eating the scraps from human camps was safer than the wolves hunting the game themselves. But to approach the camp the wolf had to change its behavior. It had to overcome some of its fear of fire. It had to adapt to act in a friendly, placating way to humans. It had to evolve to look less threatening to humans—smaller teeth, smaller mouth, higher domed skull, bigger eyes, more happy tail wagging and less snarling. In short, the wolf had to evolve into a dog. The hypothesis is that the domestication of dogs was a convergence, humans learning how to get on with dogs, dogs evolving to get on with humans. Subsequent domestications may well have been more deliberate, with the example of dogs being there to show humans what could be done.

But anthropologist Pat Shipman believes there is more to it than that. Humans, she contends, are uniquely pre-adapted to understand animals, and evolved to enhance that ability. This may be related to humans much greater abilities to understand social interactions among others, compared to the other apes, which we will come back to shortly. Whether Homo was pre-adapted to it or not, domestication of animals, understanding plant growth cycles and hence the domestication of plants, leads to trying to control them. Achieving that is the creation of a genuine technology, a linked series of inventions that provide more than the sum of their parts. This is agriculture. Once agriculture became a fixed part of human culture, more food could be produced by the labor of one individual than was needed to keep that individual alive. This led to divisions of labor, then to the social stratification, elaborate cultural structures, and highly coordinated social behavior that we collectively refer to as civilization.

With civilization came construction of buildings and weaponry, which depended on smelting ores to create metal objects. This skill extended the more ancestral crafts of creating pottery, paper, cloth, and other objects from natural materials. Using fabricated objects and domesticated animals, humans began to control and impact their environment to an extent far exceeding that of any other species. At this point, technology had arrived.

Technology became advanced with the application of mathematics and scientific insights into human endeavors ranging from agriculture to space travel. Machines were built with mathematical precision, and eventually for the purpose of computation, with today's information processing abilities comparably in speed to the human brain, if not yet in complexity.

11.5 Pre-conditions of Technological Intelligence

We can conclude on a list of possible enablers for development of technological, human-style intelligence. It is a short list (Table 11.1), however.

Obviously, some sort of complex information processing is needed, but that is not enough. Orca are smart, and can cooperate to manipulate their environment when hunting, as illustrated by stunning pictures of a pod of orca causing a wave that tips an ice-flow on which a seal has taken refuge. But orca cannot manipulate their environment beyond making waves. While dolphins can be trained to carry objects, and some carry sponges on the beaks in the wild (no-one knows why), that is the limit of their ability. So no matter how smart they are, they cannot make the simplest tool. So some way of dexterously manipulating the environment around you is required.

Table 11.1 Potential prerequisites for technological advanced intelligence

Resource/ability	Reasoning
Neural complexity	The species has to have the ability to evaluate options, and envision structures and functions of objects which are not yet manufactured. These abilities have to become quantitatively and qualitatively, because the ability to produce something with precision is needed for the fabrication and control of technologically advanced instruments
Manual dexterity	An organism must possess the ability to make use of the planet's material resources and to control its energy sources. In order to be able manipulating them in precise ways, a high degree of manual dexterity is needed. Several paths to accomplish this exist. For example, it can be accomplished with appendages such as tentacles (octopus) or with individually controllable digits like fingers (primates)
Controllable energy source	Without harnessing some kind of external energy source the ascent to advanced technological intelligence is difficult to envision. In case of humans, the role of fire was critical as it allowed some protection and partial independence from local environmental conditions. Its power was also used for smelting metals. Later on other energy sources became controllable as well and were added to the human repertoire (e.g. wind power, electricity, nuclear power)
Social interaction	Associated with the jump from tools to technology, the social structure allowed exchange of objects (trade), and then of ideas, between non-relatives. No civilizations would have been able to ascend without the group dynamics and social interactions observed in humans

Elephants have an astonishing dexterity in their trunks and parrots can manipulate natural and artificial materials with their beaks to a great extent, but neither of these two animals is capable of the type of micromanipulation required to thread a needle. However, then (almost certainly) *Australopithecu*s could not threat a needle either. This type of dexterity evolves when the animal needs it. There is no need for the manual dexterity we see in humans as long as a species has not started to make tools. As we mentioned about, several species of primates have the skill, strength and dexterity to crack rocks. The limb structure of primates that enables them to throw objects, like stones or spears, was a critical competitive advantage for the first humans, gathering in groups, and hunting big game. However, as we pointed out before, elephants can also throw objects.

Cephalopods, particularly octopi, have both complex nervous systems and manual dexterity, and evolved several hundred million years before the Great Apes. Why did they not develop advanced technology? Of course, you cannot have fire underwater, but perhaps you could utilize thermal vents on the seafloor to supply concentrated heat energy? However, that heat energy is not an as easily portable and controllable energy source as is fire on land. The marine environment may thus present an energy challenge for the development of technology that has not been overcome in 400 million years of evolution. On the other hand, you can make tools, grow crops, make nets and farm fish without fire or any other form of external energy, at least in principle. But even that was not achieved and no marine organism is known to have ever existed using this strategy. Possibly, the viscosity of water is another factor that makes the development of technology harder. As anyone who has tried to wade through waist-deep water will know, it is very hard to push something fast through water. Could you flake flint underwater? Probably not. But then there could be other resources that would make good tools that cephalopods could use and we cannot. The long strands of kelp seem pre-ordered as the basics for rope.

However, cephalopods are all solitary—none of the smarter cephalopods are social animals. If the hypothesis that exchange of things, and then of ideas, is the catalyst necessary to take a species from tools to technology, then cephalopods do not have what it takes. So a cooperative social structure is needed.

11.6 Why Has Technology Arisen Only Once in Life's History on Earth?

This still leaves many species that could have evolved technological intelligence over the past 100 million years or so. Technology is clearly advantageous. Unlike the other great apes such as chimpanzees, gorillas, and orangutans, we seem pathetically weak and dependent on artificial things, such as clothing, shelter, and the use of tools, and would die in nature quite quickly without them. But nevertheless we flourish, and the more sophisticated our technology becomes, and hence the more dependent on it we become, the more we flourish: we have become what Andy Clark calls a natural-born cyborg, a fusion of an evolved species with its technology. Humans and tool use co-evolved, meaning increasing tool use spurred brain development and vice versa. The fossil record would support such hypothesis as it indicates first chipped stone tool technologies existing already at least 3.3 million years ago. The evolution of one branch of the primates toward larger brains and tool use could have even started before the rise of the hominids, and eventually resulted in the *Homo sapiens*. From crude flint axes to the birth of agriculture, each step in technology has resulted in an increase in the human population and its spread across the planet. For us, at least, technology has paid huge evolutionary dividends. So why are humans the only ones that achieved technology?

There are two major steps along the path we have outlined above. Firstly, an enhancement of the tool-making abilities of the common ancestors of the great apes and humans. In the human lineage, tool making continued to advance, slowly at first through the australopithecines, and then faster when the genus homo came along. In the great apes tool use remained sophisticated but static. Chimps, bonobos, gorillas and orangutans all show similar levels of abilities to use tools today, albeit very different tools and behaviours as would be expected from their different ecologies. Chimps show different tool use in different environments, but they only use one type of tool, they do not combine or innovate. Enhanced tool use was associated with a modest increase in brain size. The second step was the discovery of exchange and specialization, which occurred in *Homo sapiens* between 100,000 and 200,000 years ago. This was also accompanied by a substantial increase in brain size. Brains are not easy organs to make and run. The brain of a modern human consumes about 20% of the human's resting energy consumption, even though it is only about 2.5% of the body's mass. It is also illogical that a biped should develop a huge head to hold an exceptionally large brain. This is what Timonthy Taylor from the University of Bradford in the United Kingdom calls the Smart Biped Paradox. Evolution should have favored retaining a smaller size cranium when early humans adopted an upright posture. Bipedal stance means the pelvis changes, narrowing the gap through which an infant must be born. Yet evolution pushed forward maximizing brain size with all the associated consequences of hard labour, stressful childbirth, higher damage and fatality rate among mother and baby at birth, and infants that are born before they can do even the most basic of tasks. Chimpanzee babies can cling onto their mother's fur and climb onto their backs within hours of birth. Human babies need carrying for months, they are not as capable as newborn chimps or gorillas or orangutans until 6 months' old. Yet evolution pushed on for growth in brain size in humans, so the advantages must have outweighed the disadvantages, and the advantages seem clear, at least in retrospect. Better tools meant more food, easier hunting and gathering, better defense. And exchange brings all the advantages of specialization, and gathering inventions from as far as your communication routes will allow.

Given that, it seems puzzling that technologically advanced life has only arisen once during the natural history of life on our planet, which spans several billion years. This may be even more astonishing given that the first exceptionally intelligent life occurred with the cephalopods on our planet already several hundred million years ago, and from there on in very different clades of life many more times (e.g. cetaceans, parrots, and primates). There are social apes and solitary apes—if there was benefit to developing a social intelligence like ours, surely a squid or an octopus could have trodden that evolutionary path sometime in the last 100 million years? Intelligence could have arisen in other, large land animals (Box 11.1)—kangaroos, for example, are large, social, and have manipulative hands, even if they are herbivores and so less likely to evolve high intelligence (however, there existed carnivorous kangaroos in the past).

There are different routes to address the question. One hypothesis is that technologically advanced life requires a list of parameters that need to be met for technologically advanced life to arise, and the hominids were simply the first animals for which all these parameters were met. On land, of the highly intelligent animals, only primates have the manual dexterity to manipulate objects and materials with precision, and the great apes, of which *Homo sapiens* is a member, are among the largest of the primates and hence have the largest brains. But this begs the question of why those features of large size and manipulative ability evolved in the primates and no other lineage.

The bottom line is that we do not know why only humans have evolved technological intelligence. As a result, it is highly controversial whether a technologically advanced intelligent being, functionally equivalent to a human (or superior) would eventually arise on some other planet. Carl Sagan, the most famous astrobiologist, felt convinced that other intelligences would arise on other worlds. He thought that there may be many different evolutionary pathways to reach technologically advanced intelligence, with each of it perhaps being unlikely, but that the sum of the pathways may be nevertheless substantial. He also felt that a basic principle in biology is that it is better to be smart than stupid and that there is an overall trend toward intelligence in the fossil record. The latter point was vehemently refuted by the evolutionary biologist Ernst Mayr. In his view most of Earth's biosphere is rather "unintelligent" and there does not seem to be a general tendency toward greater intelligence. He was, of course, correct—the average intelligence of all the organisms on the Earth is low, as almost all are single celled organisms. Nevertheless, the *maximum* intelligence has increased over geological time. Maybe humans arose today simply because it takes half a billion years for those simple, Ediacaran organisms to evolve such that the smartest animal on the planet starts to discover the value of banging rocks together.

Box 11.1 Questioning the Paradigm

Let's question one assumption we have made throughout this chapter. We think the assumption is right. Every serious scientist thinks it is right and it is the paradigm. And yet... are we actually the first technological civilization on Earth?

We know that Neanderthals did not build cities, dam rivers or fill the atmosphere with carbon dioxide. We would see traces of the dams and cities, and the last ice age would have ended 50,000 years early if they had developed a power-hungry industrial civilization like ours. But the artefacts of civilizations disappear quite fast. Alan Wiseman, in his book 'The World Without Us', documents how fast the artefacts of human civilization would disappear. Cities crumble, farms return to jungle or forest, even vast constructions like the Panama Canal would fill with silt in a few decades. The metals and pesticides we load into the soil would wash away in a few millennia. The plastic trash that seems so permanent a feature today will degrade in decades or centuries if exposed to sunlight, probably in around 100,000 years if buried in ocean floor sediment. The great pyramid of Khufu would be a low, unrecognizable pile of pebbles and sand in a few 100,000 years, Mount Rushmore, carved in much harder granite, would erode to look like just another mountain in under 7 million years. Humans are rarely fossilized—we burn our dead, or bury them under conditions almost designed to prevent fossilization. The only recognizable artefact we would leave after 10 million years would be our spacecrafts on the Moon and on Mars.

Some of the smarter dinosaurs had Encephalization Quotients of around 0.2 (remember this is the mammalian scale, the average is 1, we are ~6.5). But if they had bird-like brain anatomy, they will have four to five times as many neurons per gram of brain, making a really smart dinosaur as smart as a rat or a wolf. The troodontids may have had an EQ of ~0.15, and were bipedal with forelimbs which we could imagine of being adept at manipulating objects. If they had evolved into something that built cities and fought mechanized war, razed forests, flew around the world, pumped oil, slaughtered bison and landed heroic dinosaur pioneers on the Moon, what would be left now? A layer of rock with a very odd chemical composition, a clear fossil record of the sudden extinction of a significant fraction of animal species (especially large animals), and a record in the rocks of a sudden, massive rise in atmospheric CO_2 and global temperature, which dropped back quickly over the next 10,000 years. It would look, in fact, just a little bit like the K/T boundary, the layer of clay minerals that does in fact mark the end of the age of the dinosaurs formed when a 6 mile wide asteroid slammed into the Earth near what is now the northern coast of Mexico, albeit without the relatively high levels of iridium we find at the K/T boundary, which is an extraterrestrial mineral associated with the asteroid impact.

We do not believe that technologically intelligent dinosaurs existed. But we cannot be sure. When we say 'Humans are the only species to evolve technological intelligence', we should add 'probably...'. Future geology may yet turn up evidence that technological intelligence is indeed a Many Paths process, and other paths have been trodden before.

(continued)

Box 11.1 (continued)

A Troodon, possibly the smartest dinosaur. Note its arms and hands. Credit Creative Commons Attribution 2.0 Generic License.

Since technological advanced intelligence did only develop once on our planet we don't know whether the evolution of technological intelligence is a Critical Path process, a Many Paths process or even a Random Walk event (which we consider much less likely but cannot exclude at this time). Thus, it is unclear whether a second Earth elsewhere would eventually develop technological intelligence or what the fraction of worlds would be where this is the case. The likelihood of visitors, the evolution of technological intelligence, cannot be evaluated today. However, based on Earth's natural history and the time it took for evolutionary advancements needed to achieve technological intelligence, we can speculate that it would likely be rare, much rarer than animal- or plant-like organisms. Many stars, particularly A, O, and F stars may not have a sufficiently long life time to develop technologically advanced life. Even planets in orbit around G stars like Earth, may have not enough time for the rise of technologically advanced life given that the habitable zone around the star is shifting with time. On our planet human life will become unsustainable in about 1 billion years, which is a huge amount of time considering human time scales, but a relatively small amount of time considering that it took Earth 4.5 billion years for the first (and only) technologically advanced species to arise. If humans had taken 30% longer to appear than they did, the Earth might have become uninhabitable to anything other than microorganisms before we evolved. Other stars like M stars have long enough life time spans and a relatively stable habitable zone, but it is not clear whether they are likely to be habitable, as we discussed in Chap. 2. Even if a planet is in the sweet zone around a star and well-protected by its atmosphere, it is still exposed to astronomical disasters such as supernova explosions, black holes, and asteroid impacts. Planets and habitable moons may indeed be rare that provide a 4 billion year time window for the development of technologically advanced life.

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Part III

Are There Visitors in the Cosmic Zoo?

12

How to Test the Cosmic Zoo Hypothesis

At the start of this book we introduced the idea that complex life evolved from simple life in a number of key steps or innovations. Our hypothesis is that all the steps in this progression have happened many times on Earth, and so are likely to occur on other worlds. In Part II of this book, we found that most of those transitions are likely Many Paths events. If the history of the Earth were played out again, the tape rewound, the same key innovations would arise, not necessarily incorporating the same biochemistry or anatomy, but providing the same functionality. So if life arises on a distant exoplanet, it will also traverse the path from simple to complex, unicellular to multicellular, and produce intelligent animals capable of tool use in its forests and kelp beds, providing the planet is habitable for long enough.

But this is just a hypothesis. In science, you work out a hypothesis to explain your observations, as we have done, but your work does not stop there. You need to test the hypothesis. You use the hypothesis to make predictions, and then go into the lab or the outside world to see if those predictions are correct. If your hypothesis keeps on making predictions that are found to be accurate, then other scientists start to accept that it may be true. The best tested hypotheses become 'theories', and are accepted as likely to be true—such as Einstein's theory of relativity or Darwin's theory of evolution. Our hypothesis is nowhere near that yet! So how do test if we are right?

We cannot test the Cosmic Zoo hypothesis today, but one day we will be able to test it. Our abilities to do so involve further development of remote sensing capabilities and the eventual visitation of suitable exoplanets and exomoons. The bad news is that this will take decades. The good news is

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that this is a research program that space agencies around the world are already pursuing, with telescopes to characterize the planets and moons in other solar systems. In addition, further exploration with telescopes and spacecrafts of the planets and moons in our own Solar System will provide valuable data. Over the coming years and decades, this advancing march of technology will reveal more and more of our cosmic neighbourhood. We are confident that, if they find life, then on many worlds that life will be complex.

12.1 Finding Life

Working out what is on a distant planet just by looking at it is hard. The amount of information that we can get by looking at a planet trillions of kilometers away is very limited. Claims that a distant world is not just habitable but is actually inhabited will always be put in terms of chance, not of certainty. The information that we gather allows us to refine our list of what worlds are more or less likely to harbor life, and thus to focus our efforts on the more likely candidates. The program we introduce here describes current and future technologies that will provide an increasingly clear picture of whether a planet hosts life, and if it does start to give clues about whether that life is complex.

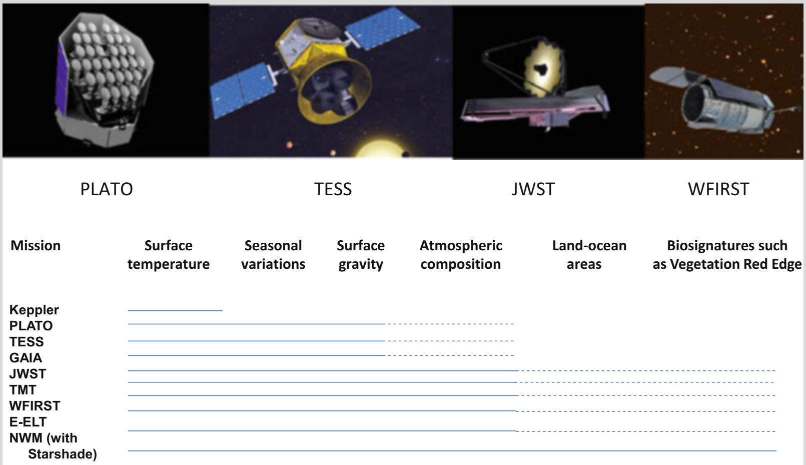
The Exoplanet.eu archive listed over 3500 confirmed exoplanets by the beginning of 2017, with an additional nearly 5000 exoplanet candidates awaiting confirmation. Most of these planets are not habitable even in principle. They are gas giant planets, or much too near to their host star, or in other ways completely uninhabitable. However the numbers are in our favour for habitability. Maybe as many as two-thirds of stars host a planet between half and twice the mass of the Earth, a size range that will be potentially large enough to keep a substantial atmosphere but not so large that they have no rocky surface. Of these about 14% are estimated to orbit within the habitable zone of their parent star, the zone in which, if they have a surface, then water would expected to be liquid on that surface. If those numbers are typical, then we can expect up to 37 billion out of the 400 billion stars in our Galaxy to have at least one planet to be approximately the right temperature and size to be habitable. Technology today can tell us this much, for planets up to thousands of light years away.

Of course, these planets may be uninhabitable for other reason such as a lack of atmosphere, lack of water or lack of organic building blocks. Perhaps the conditions on these planets were never suitable enough for the origin of life and we will see in the future many habitable planets that are uninhabited. Even if we go with the above optimistic estimates, but assume that a technological civilization only emits radio waves for say 1000 years, it would mean we have up to 10,000 radio-emitting civilizations in the Galaxy, but the average distance between them would still be at least 1000 light years. Signals sent out by us, if detected at that enormous distance, would get a reply about the year 3900 AD.

The next generation of space telescopes may be able to tell us one other critical fact, whether these planets have an atmosphere, by seeing how the gas in the atmosphere absorbs different wavelengths of light (technically, to get its absorbance spectrum). This is not a simple thing to detect. At the moment we cannot separate the image of a planet from the image of the star it orbits, so we have to analyse the light from both, and see how this varies as the planet passes in front of and behind the star. This means that we are analyzing the starlight that shines through a planet's atmosphere compared to all the light from the star. In favourable cases this can be done now, but anomalies keep cropping up. For example, the planet Gliese 1214b is 42 light years from Earth, it is larger than Earth and orbits a star smaller than our Sun, and so we should be able to get a spectrum of its atmosphere. But we cannot. Is this because the atmosphere is full of clouds (if so, we do not understand why), or because it has no atmosphere (if so, where has it gone)? In the future, better instruments may resolve this particular conundrum, but others will certainly arise. Finding out information about the existence of a thin layer of gas around a planet hundreds of trillions of kilometers away is not easy.

If we are lucky, then we will be able to say something about the gases in a handful of Earth-sized planets around nearby stars, and if we are very lucky indeed they may show signs of life. Detecting 21% oxygen in a planet's atmosphere, like we have on Earth, would be such a find. If we are less lucky, then finding out the composition of the atmospheres of Earth-sized planets will have to await the generation of space-based and ground-based telescopes currently being planned but not due to be launched until the late 2020s. Currently we are limited to determining important orbital and physical properties of exoplanets with telescopes, such as the HARPS (High Accuracy Radial velocity Planet Searcher, in operation since 2003) and space-bound instruments such as Kepler (in operation since 2009), with limited capabilities. More powerful and sophisticated instrumentation is needed to determine additional critical planet parameters to determine how "Earth-like" a planet actually is. A brief overview of such planned space missions is provided in Box 12.1 and a more daring vision of an approach for the more distant future in Box 12.2.

Box 12.1 Some Future Space Missions and Their Abilities to Characterize Exoplanets



Keppler is currently in operation, PLATO, TESS, GAIA, JWST, WFIRST, and NWM are next-generation planned missions, TMT and E-ELT are under construction and should be operational within the next decade. NWM with a “starshade” is in the proposal stage. Deploying a large occulting “starshade” in combination with one of the telescopes is especially promising (Figure12.1), because it would allow to isolate planets from their host stars. With the help of spectroscopy the isolated planet’s chemical composition of its atmosphere and surface could be determined, while photometry would allow for the detection of oceans, continents, polar caps and clouds. Images credit NASA, ESA, and CSA.

Abbreviations used: PLATO (PLAnetary Transits and Oscillations of stars), TESS (Transiting Exoplanet Survey Satellite), JWST (James Webb Space Telescope), TMT (Thirty Meter Telescope), WFIRST (Wide Field Infrared Survey Telescope), E-ELT (European—Extremely Large Telescope), and NWM (New Worlds Mission).

One of the inherent limitations of all the methods used today to study exoplanets is that we cannot actually see them, we can only see the star and planet as a combined dot. Technologies currently in the early planning stage will overcome this, and allow us to see star and planet as separate dots. The technical hurdles are formidable. As seen from Earth, Gliese 1214b in the constellation Ophiuchus is only separated from its star by the thickness of a human hair as seen from about 25 kilometer away. But we know now how this could be done, in principle, and initial experiments are under way to see if the principle can be translated into practice. One particularly daring idea is to float a shield called a starshade in front of a telescope in space to block out the light of the star, so only the light from the planet reaches the telescope (Fig. 12.1). The starshade has to be tens of meters across, and fly in exact formation with a space telescope but tens of thousands of kilometers away from it. This would

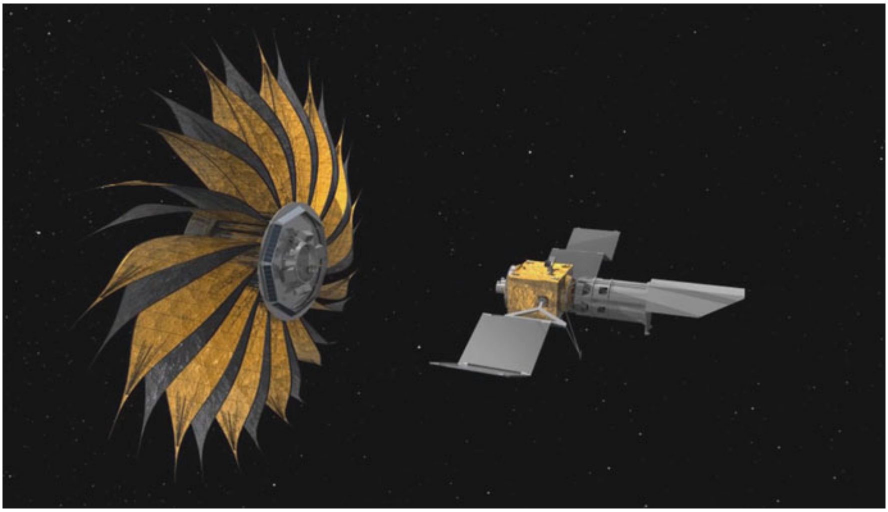


Fig. 12.1 The starshade has to be exactly aligned with the telescope to reveal information whether the observed exoplanet is *Earth-like*. Credit: NASA/JPL

allow us much more precise examination of a planet's atmosphere, and give clearer signs if there was life there.

We could also start to map the planet. Even though it would appear as a single dot in the telescope, that dot would change brightness and colour as it rotated and as it orbited its star. If conditions are favourable, we could use this information to get a crude map of the distribution of colour on its surface, perhaps including ice caps and major continents. Scientists are already working out the best way to do this.

Box 12.2 An Example of a Daring Vision to Observe Exoplanets

In the gravitational microlensing method the light from a faraway star and its exoplanet is bent around another star located midway between Earth and the distant star/exoplanet, which magnifies its image like a telescope lens. Italian physicist Claudio Maccone suggested that we could use our Sun, rather than a distant star, to create what might be the ultimate telescope based on the microlensing principle. To build such a "telescope", detecting instruments would be placed at a point in space where the Sun's gravity focuses lensed light from distant stars. It would produce images that separate the distant star from its exoplanet, a critical observation that is the goal of future space telescopes equipped with starshades (Fig. 12.1). And using the Sun as a lens would result in much greater magnification. Instead of a single pixel or two, astronomers would get images of 1000 × 1000 pixels from exoplanets about 100 light years, away, as good as an image on a computer monitor. However, the technical requirements

(continued)

Box 12.2 (continued)

are extraordinary. The telescope would have to be at least 550 AU from the Sun (1 AU, or astronomical unit, is the average distance from the Sun to Earth), which is well into interstellar space. Unless the spacecraft could move through space to track the target star exactly, it would only catch one fleeting glimpse of the planet as it passed behind the Sun. And to get that image, you have to point the telescope with the extraordinary accuracy of 100 picoradians (a radian is a measure of the size of an angle), which is the accuracy you would need to point a laser pointer at someone to get the spot on their chest from a distance of 5 million kilometers. But it is not physically impossible, and one day improvements on spacecrafts, instruments, or the idea itself might make it something worth trying.

A gravitational lens telescope, as envisioned by Claudio Maccone in his 2009 book *Deep Space Flight and Communications* (Springer-Praxis).

There are several chemical features of life that we could detect using these advanced methods. One is the presence of a gas in the atmosphere that is likely to be made by life, and not given off by volcanoes or other, non-living processes. In our atmosphere, all the oxygen is made by life, mostly by algae in the oceans, but also by green land plants. Volcanoes emit virtually no oxygen. It is possible for planets to have oxygen in their atmosphere for non-biological reasons, but it would be difficult to explain those non-biological mechanisms to operate on a planet with Earth's water content, temperature, and other atmospheric components, with Earth's age and the Earth's Sun. So an alien looking at Earth from 42 light years away would conclude at least that there was some very strange chemistry happening on our planet, and life would be a sensible explanation of that.

However, as we mentioned in Chap. 9, Earth has only had high oxygen levels in its atmosphere for roughly the last 540 million years. Also, we have to look for other gases as well, and these are likely to be present in smaller amounts—which makes them more ambiguous signs of life. It will take the detection of several different gases to provide even a 50:50 confidence that we have detected life. Our alien observers would be more confident that there was life on Earth if they could also detect methane in Earth's atmosphere, which is in disequilibrium with oxygen, meaning that those two compounds would react with each other (to form carbon dioxide); we would expect one of them to disappear from the atmosphere over time unless it was continuously replenished. Given the detection of oxygen only, a scientific colleague of our alien might argue that the high oxygen content may derive from the effect of radiation splitting up water molecules in Earth atmosphere, with hydrogen escaping to space and the heavier oxygen accumulating in Earth's atmosphere:

a plausible non-biological explanation of the observation if they had little information about Earth. But if that were the case, methane would be split up too. Finding both is more persuasive evidence than finding just one.

A second approach is to look for something that should be there, but is not. Earth has much less carbon dioxide in its atmosphere than would be expected from its volcanic activity, because photosynthesis continuously removes CO_2. Is this a sign that there is life? Or at least some unexpected surface chemistry that removes CO_2? We know that it is, but we only know that because we can see the life, and we know in detail how much CO_2 is emitted by volcanoes every year. Working out volcanic emission rates for a planet where you cannot even see continents, never mind volcanoes, is a tough task.

A third potential characteristic of life is its colour. This is also ambiguous. For example, life on Earth reflects light of wavelength 750–1000 nanometer very well. This is in the Near InfraRed (NIR) part of the spectrum, which we cannot see (although your digital camera can). Life's reflectance of NIR light is called the Red Edge (Fig. 12.2), because absorbance of light by plants in particular seems to come to a sharp 'edge' in the spectrum at about 750 nanometer.

On Earth the Red Edge is quite characteristic, but on other worlds it may not be. Studies of how plants might use light on a world with an atmosphere

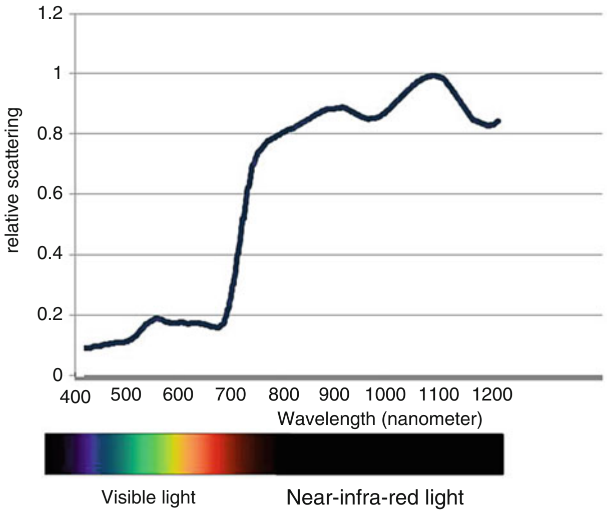


Fig. 12.2 The "Red Edge". A plot of how much light is reflected by vegetation, in this case Lodgepole pine forest in North America. The plants absorb a lot of the visible light, which is why they appear dark (with a *green* tinge), but reflect almost all the light falling on them at wavelengths longer than about 750 nanometer. Figure based on data from the US Geological Survey

made mostly of hydrogen concluded that plants there would show no Red Edge. And plants under water (i.e. plants living on 71% of the Earth's surface) have a much reduced Red Edge, as seen from above. If we could "see" an exoplanet and saw a 'Red Edge', then we might conclude there was life there, but seeing no Red Edge does not prove the opposite.

All these methods bring us ever closer to saying whether we are confident that there is life on the planet. This will be a huge step in saying whether the Great Filter lies at the Origin of Life, or elsewhere. Even finding one example of life elsewhere in the Universe would double our knowledge about how common life is. But this only tests for the presence of life, not complex life. As discussed in Part II, the chemical nature of life is pretty much the same at a large-scale level between bacteria, trees and animals. Of course, there are subtle differences. But from 42 light years, a lot of cyanobacteria do not look much different from a tree. In the foreseeable future we will not be able to say for sure whether a planet hosts complex life by remote sensing techniques only. It will already be very challenging to determine whether the planet hosts alien life at all. As we know from Earth's biota, complex larger organisms use the same type of biochemical pathways and building blocks as unicellular relatively simple life. Even if we are standing on the Moon admiring the Great Barrier Reef could we really conclude that it contains large and complex multicellular life forms without visiting? We know that simple, unicellular life can build large, complex structures, like stromatolites or microbialites (Fig. 8.3). How can we tell from a distance that the Great Barrier Reef contains corals and fish?

If we can image a planet using a starshade, we *may* be able to get hints that complex life exists on that planet. Two approaches are on the boundaries of what is possible, one detecting life on land, the other detecting life's effects on the climate.

About half the photosynthesis on Earth happens in the oceans, and is carried out by single-celled organisms. But virtually all of the other half of photosynthesis, which happens on land, is done by large, complex organisms, mostly trees but also grass. This is because the land is a hostile place for life. It is dry, exposed to ultraviolet light, and essential mineral resources are buried in the ground. In particular, organisms living on the land need to avoid dehydration and UV damage. They can live in the soil, but then they cannot easily get access to sunlight. So in adapting to land, plants became big, complex, multicellular organisms.

If we could map an exoplanet, even roughly, could we see if there was life on the land as well as in the oceans? It may be possible, if three conditions are met:

1. That we can 'image' the planet, that is we can map differences on its surface remotely

2. That we can distinguish land from sea. We may be able to do this by detecting the 'glint' of sunlight reflected off the seas, just as the Cassini orbiter detected the glint of sunlight off the polar lakes on Titan (Fig. 12.3)
3. That we can map a distinctive spectral feature that we can attribute to life on the land, and be sure we are not detecting strangely coloured rocks, dust clouds or other features.

Condition (1) is extraordinarily hard. Condition (2) is beyond any present planned capability, but is not impossible. And to be honest, condition (3) we do not know how to do. But 30 years ago we did not know how to find exoplanets (other than theoretical ideas which we had no idea how to implement in the real world), and now we know over 3500 of them.

The second approach is even more speculative. Large, land plants have a huge local effect on climate. They take water from the soil and evaporate it through their leaves (a process called evapotranspiration), and also release aromatic chemicals into the air. Both effects increase rainfall over large forests, especially in the tropics; tropical rainforests literally make their own rain. This

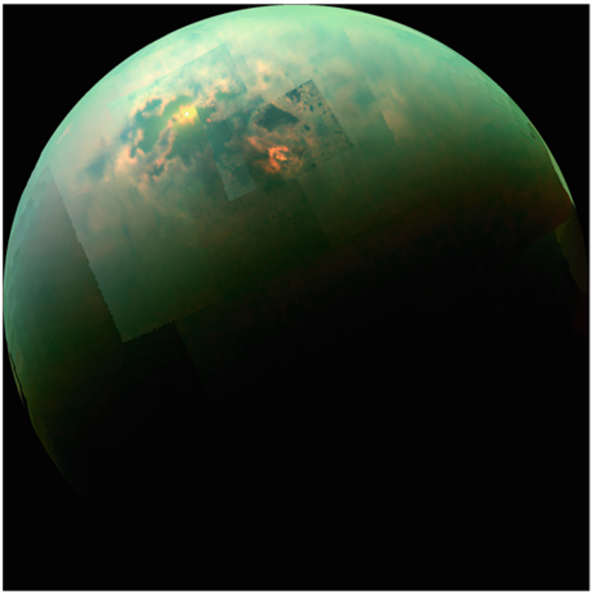


Fig. 12.3 Near-infrared, color mosaic from NASA's Cassini spacecraft showing the Sun glinting off of Titan's north polar seas. The sunglint, also called a specular reflection, is the bright area near the 11 o'clock position at *upper left*. This mirror-like reflection is in the south of Titan's largest sea, Kraken Mare, just north of an island archipelago separating two separate parts of the sea. Credit: NASA/JPL

changes the pattern of rainfall on Earth, alters the global cloud distribution, and cools the land. Trees can do this because they have a very large surface area, much larger than the ground they are growing on. In theory, we could detect such an effect on another world.

Axel Kleidon and his colleagues at the Max Plank Institute compared models of the Earth, one in which forests only covered a minimum of land area ("Desert world"), and one in which they covered a maximum ("Green planet"). They found that the two models differed by as much as 8 °C in land surface temperature in some regions of the planet, and an average of 16% more cloud over land. But the global averages did not differ much (0.3 °C lower average temperature, 2% more cloud cover), so detecting the effects of forests would require detailed mapping not just of the surface but its temperature and weather. We would also need a complete climate model, and knowledge of the atmosphere and the chemistry of the planetary crust. We do not have such detailed knowledge even for Mars.

These are extremely speculative concepts, and even if they work will only give hints of the existence of multicellular plants. Life on such world might host as rich an ecosystem as the African Savannah, or might only host mosses and lichens, or we might be mistaken and all we are detecting is bacteria being more capable than they are on Earth. Even doing this will require technologies currently only on the drawing board. But if these are developed, built and launched (most of them require space telescopes), it will not be the end. In the further future, we are confident that even more astonishing technologies will be developed. Would Galileo or Newton have imagined it was possible to see volcanoes on the moons of Jupiter or image the rings of Saturn not as a disc but as ten thousand streams of rocks and ice particles? But what those technologies could be we cannot dare say today, and they will always be fighting the fact that we are light-years away from the planets we want to study. So after studying our candidate planet from afar our next step has to be to eventually visit the alien world.

12.2 Site Visit

A thorough astrobiological investigation requires that you become close and personal with your object of interest. There is only so much you can achieve with remote sensing or even with an orbiter buzzing like a mosquito around your target planet. Ultimately, confirmation that a planet hosts complex life, and indeed confirmation that it holds life at all, must come from close examination of the planet, including sampling its surface. That means going there.

The problem, of course, is that nearly all the potential targets are so far away. The closest Solar System is the Alpha Centauri system being about 4.3 light years away from Earth, which is 40 trillion kilometers. The Alpha Centauri system is a triple star system containing the red dwarf star Proxima Centauri which may host a habitable planet, called Proxima b. A few years ago such a journey to Proxima Centauri by a robotic probe would be all but out of question; the Voyager spacecraft, for example, would take about 80,000 years to reach that distance (neither of the two Voyager probes will ever get to Proxima b, because they are going the wrong way).

However, today such an anticipated mission appears to be much more promising. One reason is that spacecraft technology has become so much more compact since the days of Voyager. This is exemplified by the growth in microsatellites like Cubesats, which pack a single satellite function with all its power, control and communication electronics into one unit, typically 10 × 10 × 10 centimeter in size. This small size makes them very cheap compared to other space missions.

The other is innovative propulsion systems. Conventionally a rocket had to be big to carry its fuel along with it. But what if you left the engine on the ground? This was an idea pioneered by space scientist Robert Forward in a project called Starwisp in 1985. The spacecraft would be a radio antenna, and the engine a battery of masers based here on Earth (or more likely on the Moon). The spaceship could reach 10% of the speed of light, getting to Proxima Centauri in 43 years. The idea was updated by NASA scientist Geoff Landis in 2000, and enthusiasm for it re-kindled, by the teaming up of internet investor and science philanthropist Yuri Milner and famous physicist Stephen Hawking for a Breakthrough Starshot project to develop a new propulsion system to reach 20% of light velocity. Yuri Milner and Stephen Hawking now suggesting lasers rather than masers, which could double the speed and halve the journey time. Thus, a journey to Proxima b would be feasible in principle in possibly less than 20 years, i.e. within a generation. Interest in the journey outside of our Solar System has also increased as evidenced by the 100 year Starship Initiative funded and supported by NASA and the Department of Defense (USA) (http://100yss.org/), which has the objective to make interstellar travel a reality within the next 100 years.

Again, this is technology well beyond what we could build today, and possibly beyond what we are willing to build. What nation on Earth would be comfortable with the idea of another nation building a laser battery capable of 100 gigawatt output? (for comparison, laser pointers typically output a few dozen milliwatts, i.e. a trillion times less power—a 1000 gigawatt laser facility would release every 10 minute as much energy as the atomic bomb detonated over Hiroshima). For this reason, the launch lasers might have to be sited on the far side of the Moon, where they could not, even in principle, ever be turned on the Earth.

But there may be a nearer solution to at least part of the question of where the Great Filter lies. Our own Solar System contains marginally habitable planets and moons other than Earth. None are as suited to Earth life as the Earth is, but then life on Earth is adapted to its home planet, not to another world, so it is inevitable that other worlds will be less hospitable to our life. But if we could find life on another body in our own Solar System, we could go there and sample it. If such life existed, it would be a very strong argument that Earth life was not an incredibly lucky Random Walk event, but that the origin of life was also a Many Paths process, even if those environments were too harsh, limited or transitory to allow complex life to develop. So before we consider a mission to Proxima b, we should consider missions to Mars, Titan, and Europa (Fig. 12.4).

Mars—is the only planet other than Earth on which a life detection experiment has been conducted. The Viking landers carried out several experiments on the Red Planet in 1975 that explicitly searched for the chemical signature of life. Unfortunately, the results were inconclusive. Most scientists agree that Mars was a habitable planet 4.5-4.0 billion years ago when Mars was warmer and wetter, with a thicker atmosphere than today and plenty of liquid water being accessible on the planetary surface. Life may have originated under these conditions, which were similar to Earth at that time, or it may have arrived from Earth via asteroid impacts, colonized Mars, and later adapted to Mars' changing environmental conditions (or, as we mentioned in Chap. 3, life might have originated on Mars and colonized Earth). About 4 billion years ago Mars became increasingly dry, cold, salty, and exposed to high doses of radiation. Any life on the Red Planet would have had no choice but to retreat

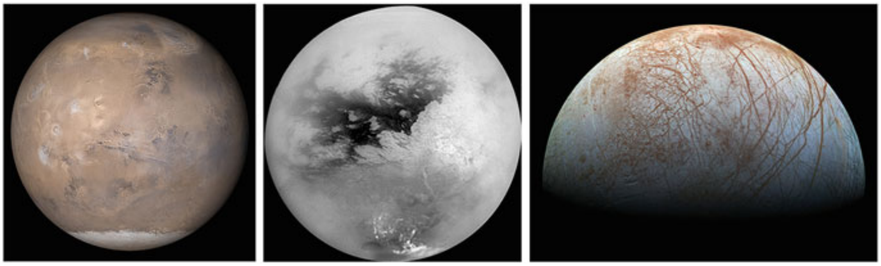


Fig. 12.4 Mars, Titan, and Europa (from *left* to *right*). They are of great astrobiological interest because they might be hosting life. Credit: NASA

to environmental niches such as lava tube caves or the geothermally heated subsurface, or if it remained in the near-surface soil, adapting to retrieve water from the atmosphere rather than from liquid water pools on the surface, which became increasingly scarce. We can observe this type of adaptation to dehydration, loss of surface water and increasing exposure to sunlight in the driest regions of Earth. In the core of the Atacama desert in Chile, cyanobacteria and other bacteria are still hanging on using special adaptation techniques, despite an average rainfall of less than one millimeter per year. Bacteria live inside rocks to protect themselves from radiation and using deliquescence to get water, a mechanism by which the salt in the rock extracts water from the atmosphere until it dissolves in the absorbed water and forms a solution, providing a suitable habitat for microbial life. This is also a strategy we would expect for life on Mars if it still exists there (Fig. 12.5).

We do not know whether current conditions on Mars are suitable for life, but the information we have about the planet's first half billion years, indicate

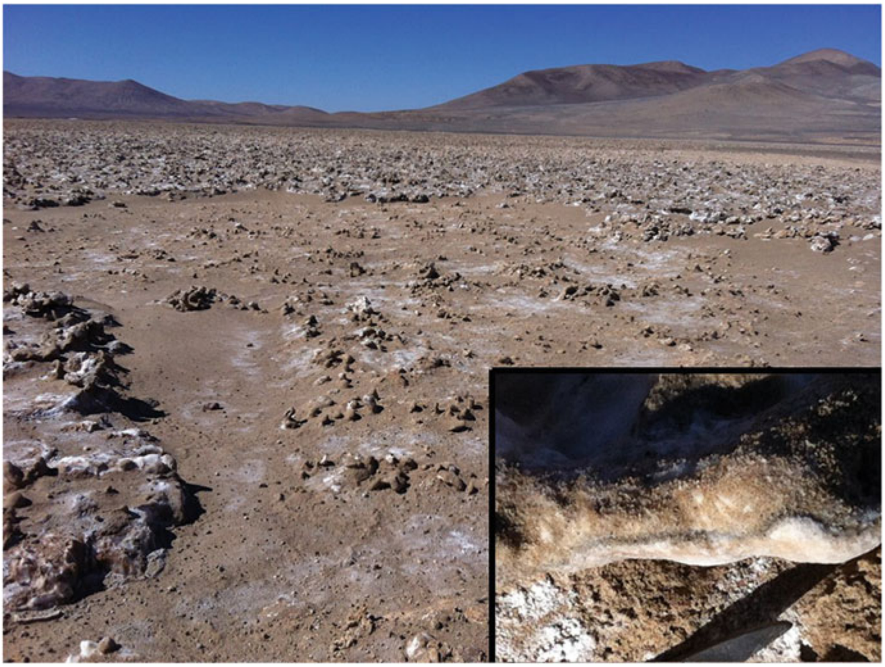


Fig. 12.5 Salt pan in the core of the Atacama desert near Yungay, Chile. The salt rocks contain living microorganism that use the rock as protection from UV radiation and the salt to extract water from the atmosphere. The dark band within the rock (see insert), which is about 5 centimeter in length, is the pigment scytonemin, indicative for the presence of cyanobacteria

that Mars was habitable at that time, with a significant atmosphere and surface water in lakes and oceans. Habitable conditions on Mars probably did not last for long enough to allow the evolution of multicellular life, or life that is large enough to be visible with the naked eye. However, astrobiology has taught us to expect the unexpected. It is not impossible that there could be multicellular life on Mars. On Earth we find nematodes, roundworms that inhabit an astounding range of environments, in some of the driest and coldest regions on Earth, regions that have similar temperatures and water availability as some of the more clement, life-friendly places in the subsurface of Mars. Aside from such a stunning and unexpected finding, even the discovery of transplanted life from Earth to Mars many billion years ago, would further our insights about the plasticity and power of evolution and life's ability to make a living in even the harshest of conditions. The discovery of a separate origin of life on Mars would be even more valuable to our quest, underlining that the origin is not a unique event and that the Great Filter is less likely to be located at the origin of life stage.

Titan—is the only moon in our Solar System with an atmosphere and large, stable bodies of liquid on its surface. It has a substantial atmosphere, 50% denser than Earth's atmosphere at the surface, with nitrogen and methane as the main compounds. The surface of that icy moon harbors extensive lakes, which do not consist of liquid water but of a mixture of methane and ethane, solvents that readily dissolve many organic molecules. Some simple organic molecules, the building blocks of life, are also common on Titan, occurring there in varying diversity and complexity. It has been speculated that life may exist on Titan, a conclusion also shared by a National Academy of Sciences (USA) report in which the statement was included that "the environment of Titan meets the absolute requirements for life, which include thermodynamic disequilibrium, abundant carbon containing molecules and heteroatoms, and a fluid environment" and further concluded that "this makes inescapable the conclusion that if life is an intrinsic property of chemical reactivity, life should exist on Titan."

The major problem that life may have on Titan, however, is that its surface is a very chilling –179 °C. In general, higher temperatures promote faster chemical reactions. Any chemical reactions would happen very slowly on Titan, and most of them requiring an extra push of energy to happen at all. This limitation may be overcome at specific environmental niches on Titan, for example at the bottom of a geothermally heated hydrocarbon lake or at a recent meteorite impact (Fig. 12.6), which could keep water-ammonia slurries liquids for ten thousands of years, as Carl Sagan pointed out more than 20 years ago. The most exciting thing about the exploration of Titan is that

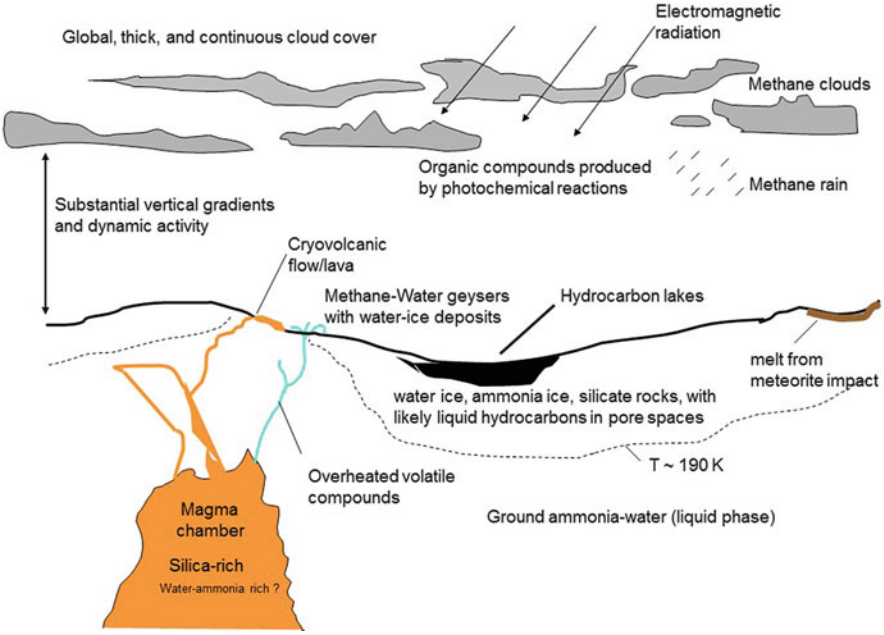

Global, thick, and continuous cloud cover
Electromagnetic radiation
Methane clouds
Organic compounds produced by photochemical reactions
Methane rain
Substantial vertical gradients and dynamic activity
Cryovolcanic flow/lava
Methane-Water geysers with water-ice deposits
Hydrocarbon lakes
melt from meteorite impact
water ice, ammonia ice, silicate rocks, with likely liquid hydrocarbons in pore spaces
T ~ 190 K
Overheated volatile compounds
Ground ammonia-water (liquid phase)
Magma chamber
Silica-rich
Water-ammonia rich ?

Fig. 12.6 Environmental conditions on Titan, Saturn's largest moon (schematic). Titan is an exotic world with a methane hydrological cycle, including methane clouds and hydrocarbon lakes consisting of liquid methane and ethane

the discovery of life on this moon would certainly mean the discovery of a separate genesis, because of Titan's exotic environment conditions (by Earth standards). Any life on the surface of Titan must be chemically so different from life on Earth that the two lifeforms would be extraordinarily unlikely to share a common origin. We would not expect that complex life could exist, however, due to the energetic limitations. But even if Titan would not be a host for life, Titan would be a great natural laboratory on how far complex chemistry can advance toward biology in an environment that is so different from Earth.

Europa—is one of the four icy moons of Jupiter, and it harbours a large liquid subsurface ocean that in principle could host multicellular life and life that may be visible to the human eye. Europa is one of the many icy moons in our Solar System. There are other icy moons such as Encedalus, Ganymede, and Callisto that can also be considered as candidates for possibly harboring extraterrestrial life in subsurface water layers. Perhaps even Pluto has an ocean of water beneath the surface. We focus here on Europa because it is the most promising icy world for finding life. The cracked eggshell nature of its icy crust provides glimpses of the internal activity of Europa, which is kneaded by tidal forces and keeps the subsurface ocean liquid. The internal activity of Europa is also manifested by ridges on its surface, which resembles the mid-ocean ridges on Earth, and may indicate the presence of an icy analogue of plate tectonics and an active recycling mechanism of potential nutrients.

Europa's subsurface ocean is thought to be in direct contact with the rocks of its mantle, thus making likely the presence of hydrothermal vents similar to oceans on Earth (Fig. 3.2). As pointed out in Chap. 3, many scientists currently think that life on Earth originated at these type of vents. If so, life on Europa may have originated at these vents as well, perhaps even using various types of energy sources (Fig. 12.7). Most intriguing, on Earth we find not only microbial life at these vents, but also a macrofauna of relatively complex organisms such as tube worms, snails, and the occasional deep sea octopus. Can a similar analogy be drawn to Europa?

Europa is smaller, with less energy and possible nutrients available than on Earth, thus a biosphere would be less dense and diverse. Louis Irwin and one of us conducted a modeling exercise to test that. We assumed molecular hydrogen as energy source for putative life at subsurface vents on Europa. Hydrogen

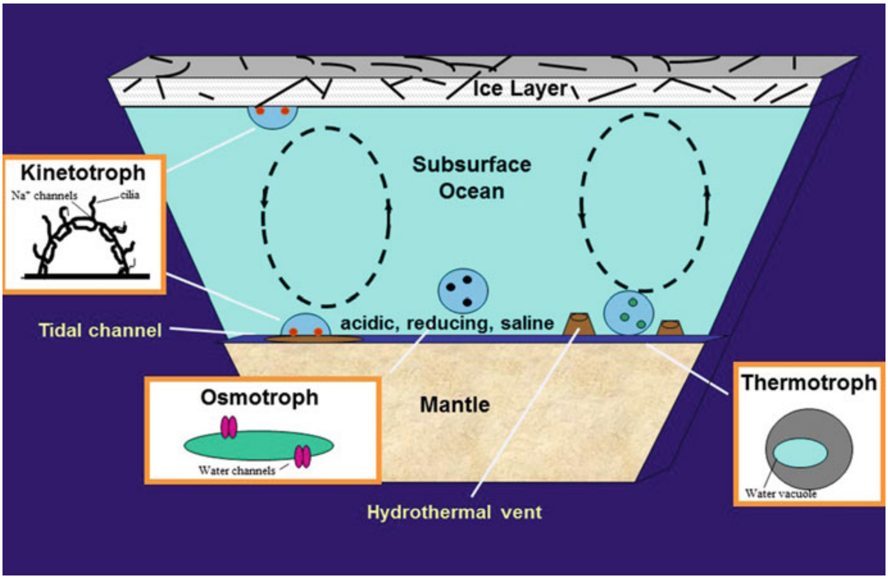


Fig. 12.7 Hypothetical microorganisms in Europa's subsurface oceans, schematic. The kinetrophic organism would obtain energy from kinetic energy such oceanic currents, the osmotroph from salinity gradients, and the thermotroph from thermal gradients. More information on the hypothetical life forms can be found in *Life in the Universe: Expectations and Constraints* (2nd edition), by Schulze-Makuch and Irwin (2008)

is created by reaction of water with hot rocks on Earth (a chemical process called serpentinization), and the study assumed the same process on Europa, scaled down from the rates on Earth to the smaller size of Europa. Life on Europa would utilize the reaction of hydrogen and carbon dioxide to make water and methane (methanogenesis) to extract energy.

The conclusion was that such a methanogenesis-supported ecosystem on Europa could in principle support enough biomass to feed one predating organism the size of a brine shrimp per Olympic size swimming pool. Other modeling studies using different energy-obtaining reactions resulted in biomasses within an order of one or two magnitudes of this estimate. The modeling exercise does not say anything about the likelihood that the methanogenesis reaction actual occurs or not, but it shows that in principle enough energy is available to support a diverse and complex biosphere. The obtained results show that the total biomass would still be low compared to terrestrial environments, but nevertheless indicates that in principle complex life could exist in Europa's subsurface ocean.

The biggest unknown is the chemistry of the subsurface ocean, which is essential to know whether the ocean is really habitable. The coating of some of the geological features on Europa's surface with salts (which were detected by the Galileo mission to the Jupiter system) seem to indicate that the ocean is not highly acidic, and contains some dissolved material which may include organic compounds, providing some optimism that the subsurface ocean is indeed habitable. Given our lack of knowledge, space missions are desperately needed to find out. Recently plumes of water ejected into the thin Europan atmosphere have been detected. These plumes probably originate from the subsurface ocean, at locations where the liquid ocean is close to the surface (e.g. the so-called Chaos region). The existence of the plumes, and hence the thinner areas of crust, would make such an endeavor look easier than thought just a few years ago.

If Europa's subsurface ocean is hosting a biosphere, it would likely be very distinct from terrestrial life, and be of a separate origin. The Jovian system of satellites formed when the Solar System formed, and well before the Earth was sterilized by the impact that formed our Moon. Europa would have been capped with ice from early in its existence. The chance of life travelling from Earth to Europa or vice versa is vanishingly small. If we find life in the oceans of Europa, we will be very confident that its origin is separate. To find another world within our Solar System on which life has originated would be a powerful argument that life is a common phenomenon across the Universe.

Even more importantly, Europa has the potential of being the first test of our Cosmic Zoo hypothesis. If life did originate on Europa long ago, did it evolve further to form multicellular, more complex forms? Some of the key innovations that occurred on Earth would not be expected on Europa such as photosynthesis (there will be no sunlight below the thick ice crust), but others may have occurred instead. At hydrothermal vents in Earth's ocean we find a fauna independent of photosynthesis, which still includes some complex and larger life forms. Do we find similar animal-type life forms on Europa as well, even if they are only similar to a "humble" brine shrimp?

12.3 Ultimately Complex: The Search for Extraterrestrial Intelligence

All the tests above test for complex life, but not for technologically advanced life. As we said in our introduction of the book and also in Chap. 11, what we would really like to do is search for life like our own, life that can communicate with symbolic language, and which has the technological capability to communicate between the stars. This is SETI—the Search for Extraterrestrial Intelligence, and its more active younger brother METI—messaging extraterrestrial intelligence.

All the searches for extraterrestrial intelligent life have been uniformly unsuccessful to date. But as Jill Tartar of the SETI Institute says, this proves almost nothing. Our searches to date have looked at only a tiny sliver of the radio spectrum and a few spots in the sky. To say there are no radio-emitting civilizations out there is, she comments, like dipping a bucket into the sea, seeing no fish in the bucket, and concluding there are no fish in the sea. To do anything like a thorough search, we must expand the search enormously. There are three approaches to extending our search, and hence validating the Cosmic Zoo hypothesis in the most dramatic fashion possible.

The first is simply to extend the currently conducted search for radio signals. New initiatives such as the Allan Array, sponsored by Microsoft co-founder Paul Allan, and the SERENDIP program, aim to extend our listening powers by many factors of ten. This is still only a tiny fraction of what might be needed, but obviously is more likely to be successful than not listening at all. METI seeks to get aliens to respond more actively to us by signaling to them. However, if the nearest technological culture is more than 1000 light years away, that will take a long time. In addition, METI is very controversial as we do not know the intension and objectives of any alien visitors.

The second is to search for other fingerprints of technological civilizations around other stars. If civilizations more advanced than ours increasingly engineer not just their own planet but their entire solar system, the next generations of telescopes could detect that. There was some excitement in October 2015 when data from the Kepler space telescope, designed to hunt for planets, seemed to indicate that star KIC 8462852 was host to an irregular object much larger than any planet. Was this a huge orbiting habitat, called a megastructure? Subsequent analysis suggested that it was just a giant comet breaking up around a young star. A search for radio signals from the star detected none.

The last approach again is nearer home. If we are near to sending an interstellar probe to Proxima b, could alien civilizations have sent one to us? Hard as though it would be to find a space probe of a few kilograms among the billions of tons of orbiting rock and dust in our Solar System, its energy emissions might give it away. It might just be worth a try, especially as the same survey would map many types of rocks.

12.4 Visiting the Cosmic Zoo

The tests we describe above all belong to the future. We hope we are around to see the results of some of them, and we are confident that, if there is life on another world, in at least some of them it will evolve to complex life that we can detect with methods available in 20–30 years. But what of today? We are impatient people. We think you, our readers, also want answers now.

We cannot provide definite answers. Two key uncertainties remain. How common is life, and how common is technology.

We know that there are no other radio-emitting civilizations within our immediate corner of the Galaxy. But we have no idea whether life is common or rare. This makes the future exploration of Mars, Europa and Titan so exciting. It is not just the astonishing pictures beamed back to Earth, although those are amazing. From the red sky and dried canyons of Mars to the rivers of Titan to the icy plains and volcanoes of Pluto, every planet and moon we have visited in the Solar System has proven to be more varied and more active than anyone had previously thought. But in addition, the more we learn of these worlds, the nearer we come to understanding whether life on Earth was an extraordinary statistical fluke or something that can be expected on many habitable worlds.

Further Reading

Possible Life Within Planetary Systems Including Our Solar System

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13

The Great Filter and the Fermi Paradox

In the beginning of this book we introduced the idea of a Great Filter, something that stood between the formation of planets (which we know is common) and the existence of technological civilizations (which seems rare). We asked ourselves where the Great Filter may be and surmised that it may be located in principle at any of the many steps that have led from the origin of life to modern humanity over a time period of roughly 4 billion years.

In Part II of the book, we reviewed the key innovations between the origin of life and our own emergence on Earth. If *all* the steps described in Part II are likely, Many Paths processes, then technological species should be abundant in the Universe. But we do not see them. This problem has been known for decades, and is called (rather inaccurately) the Fermi Paradox. Robert Gray thinks that it would be better termed the Great Silence—the observation that despite all the planetary real estate that we now know is out there, we still do not have any evidence of intelligent extraterrestrial life. So where are the visitors or messages to Earth?

There is strong evidence that most of the key innovations that we discussed in Part II of this book follow the Many Paths model. If the key innovations occurred multiple times using different mechanisms but within a limited time period, then we can be very confident that this transition will occur inevitably given suitable environmental conditions. This is clearly shown in the invention of mechanisms to capture light energy into chemical energy, the invention of endosymbiosis, the rise of multicellular life and the achievement of intelligence. Other key innovations are more challenging to evaluate, such as the invention of the ability to make oxygen, which happened only once. We can

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suggest that the evolutionary path that lead to oxygenesis is made of steps that happened many times, but the overall innovation may be an example of a more difficult and hence rarer step. But overall, we feel confident that all the innovations between the origin of life and the appearance of technologically advanced life would re-occur on Earth or another planet assuming habitable conditions would persist for long enough.

There are, however, two prominent exceptions to our assessment.

The first exception is the origin of life itself, which is really due to our ignorance, despite of many decades of dedicated research in that field. We do not know how life originated on Earth, and only have vague speculations when and where it arose. We do not even know for sure that it originated on Earth (though most observations indicate that this is so). What we do know is that the origin of life was a *Pulling Up the Ladder* event. Once it originated life would have spread across the planet and removed the conditions under which other life could have originated. Especially it would have gobbled up any organic molecules as food source, and used any energy source available for its own needs, leaving none for a newly emerging independent life to exploit.

If the Great Filter is located at the origin of life, this could mean we are utterly alone in the Galaxy, maybe even in the entire Universe. Most scientists consider this unlikely. Life apparently appeared quickly on our world, almost as quickly as it possibly could arise after our world cooled down and Earth's water condensed into oceans. We are very confident that chemical reactions making organic molecules occurred in the early Earth environment, especially in promising locations such as hydrothermal vents on the ocean floor. We know that there were sources of chemical energy available, such as the redox gradients in those hydrothermal systems, the cyclic wetting and drying of seashore environments, and of course visible and UV sunlight. All of these would have been more abundant on the early Earth than they are today. There was no ozone layer to shield against UV, the Moon was much nearer and so caused much higher tides, and the Earth was probably more volcanically active. So all the ingredients were there, and from the huge number of places and millions of years of time, surely (scientists would argue), the right conditions arose somewhere.

Nevertheless, the bottom line is that we do not know, and so today we cannot exclude the possibility of the origin of life being an extremely unlikely Critical Path process, or even a Random Walk event. We do not think that the origin of life was a unique event to Earth (and most of our colleagues do not believe that either), but we simply don't know for sure.

If the origin of life is not very rare, then we have made a strong argument that we live in a Cosmic Zoo. But what most of us are interested in is not only whether there is complex, macroscopic life elsewhere in the Universe, but whether advanced, intelligent beings with language and technology exist, with which we could communicate. Only then would we not feel alone anymore in the Universe. So, does the Cosmic Zoo contain life forms with whom we could exchange notes and philosophize about our place in the Cosmos?

That brings us to the second exception to our observation that the path to ourselves is a Many Paths process. The exception is the rise of technologically advanced life itself. It has only occurred on Earth once, which might be surprising given the immense power of evolutionary innovation and biological diversity on Earth, especially judging from the success of humans as a technologically intelligent species. Tool-using animals have appeared many times, as have animals with the intelligence to solve quite complex problems, so it is puzzling that none made the next step, a step that seems so obvious to us, to a technologically intelligent species in the many billions of years within the history of life on our home planet. The absence of other technological species other than our own suggests that our intuition about what is "obvious" is wrong, and there is no easy evolutionary trajectory that would necessarily propel some members of a complex biosphere to become technologically advanced.

Could then the Great Filter be the step toward technological intelligence?

There is no shortage of species that had large brains, complex cognition, potentially dexterous hands and the sort of omnivorous or carnivorous lifestyle that is generally believed could benefit from enhanced intelligence. But none has developed technology, no smart enough dinosaur, no smart enough bird, no smart enough mammal. Why, for example, did *Propleopus oscillans*, a 2 meter tall carnivorous kangaroo weighing 70 kilograms, not evolve to become technologically advanced? Instead it became extinct. Why did the Troodontid dinosaurs not develop technology, instead of going extinct? Of course, *Homo sapiens* became nearly extinct as well. The genetic diversity in modern human populations indicates that our species was down to a few thousand individuals between 50,000 and 100,000 years ago. That genetic bottleneck has been associated by some scientists with the climatic after-effects of the Toba supervolcano eruption 75,000 years ago. Charles Lineweaver suggested just that when he pointed out that the human lineage did only originate on one of the continents of Earth (Africa) and only once. Could it be that we, *Homo sapiens sapiens* are really so special and rather unique in the Cosmic Zoo? Whether the supervolcano eruption was responsible for the genetic bottleneck or not, the fact remains that technologically advanced life originated only once on our planet and even in that one event that species nearly became extinct. Perhaps, it is just a very rare phenomenon which is not repeated on many other planetary bodies in the Universe. Maybe the Great Filter lies quite near to us in evolutionary time, in the step between complex life and technological life.

The third and least attractive option is that the Great Filter still lies ahead of us. Maybe technological advanced species arise often, but are then almost immediately snuffed out. Technological civilizations may not last long, which would help explain why we do not receive any signals from space indicative of intelligent life. We have no shortage of possible ways to obliterate our own technological culture, from nuclear war to global warming. The lifetime of a civilization may be short, because it exhausted the readily accessible resources of the planet before it can reach genuine interplanetary civilization. The civilization might then fall back on a low-energy, low-technology, surface-bound civilization, which may last for millions of years but cannot be seen from other stars.

Alternatively the civilization may crash because their technology becomes too complex for them to understand or control (coupled to this is the worrying idea that human intelligence is actually declining at the same time as our technology becomes ever more complicated, although thankfully the evidence for this is weak). Perhaps, the Great Filter is just ahead of us, and we simply do not know what challenges still await us. We barely explored our own Solar System and if civilizations at this state of technology would generally cease to exist, there would be almost no radio-chatter occurring between civilizations. We have sent 11 radio messages to the stars in the last 50 years (plus a continuous background of accidental transmissions of radio and TV signals, radar beams and other radio ‘noise’). If our radio-emitting and receiving culture only lasts 100 years, then we can only expect to get a reply from a planet within a 50 light-year distance of Earth that just happens to be in that same 100-year segment of its 10 billion year history, and the chances of that are essentially zero.

So far, all the barriers humans have thrown up against ourselves we have overcome. The nuclear war widely expected in the 1950s did not turn up, catastrophic exhaustion of resources predicted in the 1960s never happened. But as society becomes more global, interconnected and more dependent on technology, can this continue? The future is the pessimist’s location for the Great Filter, when we at last do something to ourselves or to our planet that even our own ingenuity cannot overcome.

Or maybe our assumption is wrong, and the failure of SETI to detect other technologies is a failure to look in the right way. There is no shortage of ideas about why we have not found extraterrestrial life with our radio searches. It may be that technological life is long-lived, but that it only spends a few decades or centuries at our primitive level of development where they use radio

Fig. 13.1 Human exhibit at the London Zoo, UK. Credit: Gareth Cattermole/Getty Images

waves at all. We might be trying to communicate with ET with the technological equivalent of smoke signals. Or their reasons may have nothing to do with capability to communicate, and all about desire to communicate. As we have no other alien species to compare ourselves with, we have absolutely no idea. So ideas such as a Human Zoo (Fig. 13.1), the Earth Quarantine (our ideas and behavior are so horrible than noone wants to know us) and other explanations for the Fermi Paradox are really just wild speculations, not scientific explanations.

Perhaps the solution to the Fermi Paradox is more mundane. The Great Silence we encounter might only be an artifact of space being so incredibly large. If there were a million radio-emitting planets in our Galaxy, the average distance between them will be about 200 light years. In 2017, Earth's earliest long-distance radio transmissions are only ½ the way there. Perhaps we can expect a reply sometime around the year 2400?

Where does that leave the Cosmic Zoo? We cannot know. If life can arise easily on Earth-like planets, and it is the consensus of scientists exploring the origin of life that it probably can, then we would expect that life to develop complex species on many worlds. In that case, Earth, with its diversity of animals, plants, fungi, single celled eukaryotes, bacteria and archaea, is not rare. On the other hand, we have not found any evidence for other technological civilizations.

Based on Earth's natural history and the evolutionary advancements needed for technologically advanced intelligence, particularly the requirement of stable time to evolve a complex social structure, they might indeed be uncommon. The step toward advanced technological intelligence or the time duration of an advanced technological intelligence may well be the step where Robin Hanson's Great Filter lies, and be the explanation for the Fermi Paradox.

So we should look, both for life on other worlds and intelligent, technological, communicating life. If life exists out there, then we are confident that complex life will exist on many worlds. And on some world thinking, abstracting, scientific, artistic, creative beings will arise and will wonder as we do whether they are alone. We hope we can find them, talk to them, and together explore the multitude of worlds that make up the Cosmic Zoo.

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List of Terms

100-year starship initiative A project supported by NASA and the Defense Advanced Research Projects Agency (DARPA) to achieve the capability to undertake human travel beyond our Solar System within 100 years.

Abscisic acid A plant hormone with many functions in plant developmental processes, including responses to stress.

Absorbance spectrum The fraction of radiation absorbed by a material at different frequencies of that radiation, which is mainly determined by the atomic and molecular composition of that material.

Accretion The process by which smaller particles collide and stick together. In the context of planet formation, accretion can be non-gravitational (particles 'sticking' together) or gravitational (larger bodies falling together under their mutual gravity).

Activation energy The energy that two molecules have to have for a specific chemical reaction to take place.

Acuity The ability to resolve fine image details via vision or fine spatial details via a sense of touch.

Adenine triphosphate (ATP) The molecule most commonly used in metabolism to transfer energy between one reaction and another ("energy currency"). The ATP molecule consist of adenine, D-ribose (a sugar), and three phosphate groups linked together by covalent bonds.

Aerobe An organism that generally lives in environments containing molecular (free) oxygen. An obligate aerobic organism requires oxygen for metabolism and growth, while a facultative aerobic organism can live in both the presence or the absence of molecular oxygen.

Albedo Amount of reflected solar energy from a physical body such as a planet or moon.

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Alga (pl. algae) A large and diverse group of photosynthetic **eukaryotes**, usually relatively simple and occurring in an aquatic environment, some of which are multicellular. Examples include seaweed and green, red, and brown algae.

Alpha Centauri The nearest star system to the Sun at a distance of about 4.4 light years.

Alpha-proteobacterium A diverse group of bacteria with a common ancestry based on genetic sequencing belonging to the **phylum** Proteobacteria.

Amino acids Small nitrogen-containing molecules that are the building block of **protein**s and thus a fundamental component of life as we know it. 20 amino acids are commonly used to build proteins by life on Earth, where they are connected via **peptide bonds**.

Ammonia A molecule common in gas giants and occurring as trace compound in Earth's atmosphere consisting of one nitrogen atom and three hydrogen atoms (NH_3).

Amoeba A single celled **eukaryotic** organism, which has the ability to change its shape. 'Amoeboid' means a cell that can change its shape, like an amoeba.

Amphibian Cold-blooded **vertebrate** that does not have scales, and has at least part of its life cycle in water. Examples include frogs and newts.

Anaerobe An organism, most commonly a microbe, that can only grow and metabolize in the absence or near-absence of molecular oxygen. A 'strict anaerobe' cannot tolerate any oxygen.

Antenna complexes A light-harvesting aggregate of **proteins** and pigments, with chlorophyll at its center, inside the **chloroplast**s of photosynthetic organisms.

Aphid A small sap-sucking insects belonging to the family Aphididae. An example is the garden greenfly.

Arboreal Organisms (mostly referring to animals) that live in trees.

Archaea A domain and kingdom of the **prokaryotes**, genetically and structurally distinct from the domain of bacteria, see also Box 1.1.

Archaean Geological time period from approximately 4 to 2.5 billion years ago, see Box 1.2.

Ardipithecus An extinct genus of hominins. Two fossils were discovered to date, *Ardipithecus ramidus*, dated to be about 4.4 million years old, and *Ardipithecus kadabba*, dated to be about 5.6 million years old.

Aromatic chemicals Compounds containing rings of atoms bonded together in a specific pattern, often associated with some kind of odor.

Arthropod An **invertebrate** animal characterized by a segmented body, an external skeleton and paired appendages. The **phylum** *Arthropoda* includes insects, arachnids (e.g. spiders and scorpions), myriapods (e.g. centipedes and millipedes), and **crustacean**s (e.g. crabs and lobsters).

Astronomical unit (AU) The mean distance between the center of the Sun and the center of the Earth, 149.6 million kilometers.

Atmosphere The gaseous layer surrounding a planetary body (planet, moon) or a star. Many planets or moons (such as Earth's Moon) do not have an atmosphere.

Asteroid A subplanetary object, which formed by **accretion**, usually about 10 meter–1000 kilometer across, composed of non-volatile material and in orbit around a central star.

ATP See **adenine triphosphate**.

Australopithecus An extinct genus of hominins that lived in eastern Africa between about 4 and 2 million years ago.

Autotroph An organism able to synthesize all the organic compounds it needs from inorganic compounds (such as CO_2 from the air) and an external energy source. Depending on the utilized energy source, there are **photoautotroph**s (such as plants) and **chemoautrotroph**s (such as certain bacteria).

Bacteria Very common unicellular organisms which multiply though cell fission and are **prokaryote**s.

Bacterial mat A multi-layered sheet of **bacteria**. If that sheet includes **archaea**, then this is referred to a microbial mat, if it includes **algae**, then it is referred to as an algal mat.

Bacteriorhodopsin A **protein** used by **archaea**, particularly **halobacteria**, that captures light energy and converts it via a proton gradient into chemical energy.

Banded iron formation (BIF) Rocks composed of alternating layers of iron-rich material (often magnetite) and silica (chert), deposited in the **Proterozoic** time period. Interpreted as evidence that the atmosphere at that time did not contain substantial amounts of molecular oxygen, as any oxygen present was removed by reacting with the iron dissolved in sea water to form iron oxide minerals on the ocean floor, which later was incorporated into the rocks.

Bicarbonate A molecule with one carbon, one hydrogen, and three oxygen atoms (HCO_3^-), which is soluble in water and playing an important role to keep the pH-value around neutral.

Bilatera Organisms with a bilateral symmetry, i.e. organisms whose left and right sides are approximately mirror images of each other. All **vertebrate**s, insects, and many other species have this kind of symmetry. Jellyfish, by contrast, do not.

Binary star Two stars held together by their mutual gravitational pull within one **solar system**. More than 30% of **solar system**s appear to be binary star systems.

Biological energy quantum (BEQ) Minimum amount of energy needed in a chemical reaction for a cell or organism to use that reaction to build high-energy molecules such as **ATP**.

Biofilm Any group of microorganisms in which cells stick to each other, typically adhering to some type of surface.

Biosphere A global **ecosystem** including all organisms and their relationships, plus their interaction with the rocks, solvents, the **atmosphere**, and other inorganic components of a planet or moon.

Bonobo One of the two species making up the genus Pan, the other being the chimpanzee. Bonobos used to be called Pigmy Chimpanzees, but are now understood to be a different species. Bonobos are smaller and less aggressive than chimpanzees, and noted for resolving disputes within a pack using grooming, sharing, or sex rather than aggression.

Breakthrough starshot A funded effort by the Breakthrough Initiative to achieve a significant fraction of the speed of light to reach exoplanets. The board of the Breakthrough Initiative includes Stephen Hawking, Yuri Milner, and Mark Zuckerberg and has the goal to find out whether we are alone in the Universe.

Brine A solution of salt in water, where the salt content is equal or higher than 3.5%.

Callisto Second largest moon of Jupiter consisting of a mixture of rocks and ices, which might contain liquid water deep underneath its crust.

Calvin cycle The cycle of chemical reactions in photosynthesis that builds carbon dioxide into sugars, and includes the light-independent reactions during the process of photosynthesis.

Cambrian A time period from approximately 541 to 485 million years ago, see Box 1.2.

Cambrian Explosion An evolutionary time period starting about 540 million years ago in which there appeared a large number of new marine animal species in the fossil record. Until about 50 years ago, no fossils dating from before the Cambrian Explosion were known.

Canidae Dog-like mammals which also includes wolves and foxes.

Capuchin monkey One of the New World monkeys of the subfamily Cebinae, which live in the wet lowland forests of the Caribbean coast and the dry forests of the Pacific coast.

Carbon monoxide A molecule consisting of one carbon and one oxygen atom combined with a triple bond. A colorless, odorless, and tasteless gas that is toxic to animals (including humans).

Carnivore An organism that meets its energy and nutrient requirements from a diet consisting mainly or exclusively of animal tissue, either through predation or scavenging.

Carotene An orange-colored plant pigment found in carrots and many other plants, of which several varieties exist.

Cartilage A firm tissue, softer and much more flexible than bone. In humans cartilage is the connective tissue found in many areas of the body such as joints between bones, and the outer parts of the ear and nose. Some fish such as sharks have their entire skeleton composed of cartilage.

Catalyst A chemical that promotes the reaction of another chemical without being used up itself in the process.

Cephalopod Any member of the class Cephalopoda of the **phylum** of the **mollusc**s, which became dominant during the **Ordovician** time period and include the octopuses, squid, **cuttlefish**; and Nautiloidea.

Cetacean A diverse clade of finned, carnivorous marine mammals, which includes the dolphins, whales, and porpoises.

Choanoflagellate A group of free-living unicellular **eukaryote**s, which have **flagella** and a colonial lifestyle. They are typically about 3–10 micrometer in size and are believed to be the closest unicellular living relatives of the animals.

Chemoautrotroph An organism that synthesizes all the organic compounds it needs from inorganic chemicals, using the energy extracted from those chemicals to live.

Chicxulub Locality on the Yucatan Peninsula in Mexico that exhibits a 180 kilometer wide partially submerged crater, which is probably the crater formed by the impact of the **asteroid** or **comet** that was partly responsible for the mass extinction of the dinosaurs at the end of the **Cretaceous** Period.

Chlorin ring A large **aromatic** ring which includes four nitrogen atoms. If a magnesium atom is added to the center of the ring, these chlorins are called **chlorophyll**s.

Chlorophyll The primary photosynthetic pigment involved in the capture of light energy. The capture occurs during **photosynthesis** in all plants and **algae**, including **cyanobacteria**. For more details see Box 4.3.

Chloroplast An **organelle** that contains **chlorophyll** and in which **photosynthesis** takes place.

Chromosome A thread-like structure of **protein** and a single molecule of **deoxyribonucleic acid (DNA)** found in the **nucleus** of most living cells, which carries information in the form of **gene**s.

Ciliate A group of **protozoa**ns characterized by the presence of hair-like organelles (cilia), which are used for locomotion and food gathering. Most ciliates have a free-living lifestyle.

Collagen The main structural and most abundant **protein** found in animals. It forms gelatin when boiled.

Comet Planetary objects, typically of a few kilometer across, that consist of frozen gases, and a variety of ices embedded in rock and dust.

Complex life The definition of what is complex (and what is life) is disputed, but in this book we define complex life as life that is obligatorily multicellular and, as a consequence, has a distinctive developmental program.

Corvidae A family of birds that includes the crows, ravens, rooks, jackdaws, jays, magpies, treepies, choughs, and nutcrackers.

Crenarchaeota A diverse **phylum** of single-cellular organisms belonging to the kingdom of the **Archaea**.

Cretaceous A time period from approximately 145 to 66 million years ago, see Box 1.2.

Critical Path Model A model of an evolutionary transition stating that the main reason that a transition does not happen at once there is a specific set of preconditions that have to occur, which take time to develop, before a transition can be achieved.

Crustacean Animals that usually have a hard covering, or exoskeleton, and two pairs of antennas, or feelers. Crustaceans belong to the **arthropod**s and crabs, lobsters, crayfish, shrimp, krill, woodlice and barnacles are examples of crustaceans.

Cryptophyte A group of **alga**e common in freshwater, but also occurring in other aqueous environments. About 10–50 micrometer in size with a flattened shape.

Cubesat A miniaturized satellite or spacecraft, typically of about 10 centimeter length in each dimension and not more than 1.33 kilogram weight per unit.

Cuttlefish Marine animals that belong to the **cephalopod**s (Class Cephalopoda), which are known for their ability to rapidly change their body and skin patterns for camouflage and communication.

Cyanobacteria A group of photosynthetic **bacteria** that possess **chlorophyll** and have been implicated to be responsible for the **Great Oxygenation Event** 2.4 billion years ago.

Cyborg A human-machine hybrid. This term is usually used for speculative future hybrids for which selective advantages of both human and machine are unified, though in a strict sense any human with an implant (like a pacemaker) can be considered to be a cyborg.

Cytoplasm The material inside a cell. In a eukaryotic cell this contains the organelles of a cell as well as **metabolites, proteins, RNA** and other constituents. It surrounds the **nucleus** or **nucleoid** of the cell.

Cytoskeleton A complex network of interlinking filaments and tubules that extend throughout the **cytoplasm** of a cell. All eukaryotic cells have a cytoskeleton, a few giant bacteria have a similar system, but most non-eukaryotes do not.

Deliquescence The process when a substance absorbs moisture from the **atmosphere** until it dissolves in the absorbed water and forms a solution.

Deoxyribonucleic acid (DNA) The genetic material and information carrier in all known cells on Earth. The double-stranded molecule consists of **nucleotides**, which are themselves made of sugars, phosphate and organic bases.

Devonian A time period from approximately 416 to 358 million years ago, see Box 1.2.

Diatom *Unicellular* **alga**e with transparent cell walls made of silicon dioxide (silica). They make up a large amount of **plankton** in the oceans.

Diffusion Physical process usually occurring in a gas or liquid, where molecules of one material move from an area of high concentration to an area of low concentration.

Dinoflagellate **Protists** with a **flagella** that live in water and make up a large amount of **plankton**.

Diploid A cell that contains two complete sets of **chromosomes**.

Dunbar's number A suggested limit to the number of people with whom one can maintain stable social relationships based on human limitations on cognition, usually taken to be about 150.

Earth 2.0 Common reference to a second Earth, a planet in physico-chemical and biological properties very similar or identical to Earth.

Echolocation A method used by animals to locate and identify objects via emitting sound out to the environment and listening to the echoes that return from various objects near them (similar to 'sonar' used by submarines).

Ecosystem A community of organisms interacting with each other and their physical environment.

Ectosymbiosis **Symbiosis** in which the symbiont lives on the body surface of the host, which can also include internal surfaces such as inside the gut.

Ediacaran A time period from approximately 635 to 541 million years ago, see Box 1.2.

Ediacaran fauna A unique assemblage of soft-bodied organisms, particularly animals, which flourished in the **Ediacaran** time period, just before the **Cambrian Explosion**.

Enceladus A rather small moon of Saturn (a bit more than 1/1000th the mass of Earth's Moon). Its south polar region sprouts fine water ice particles and other compounds into space, which has been interpreted as deriving from a subsurface liquid water reservoir.

E. coli *Escherichia coli*, a **bacterium** commonly found in the lower intestine of warm-blooded organisms and a model organism for all kind of laboratory experiments.

Encephalization quotient (EQ) A measure of relative brain size. The measured brain mass is compared to the brain mass for an animal based on its overall size (mass), particularly a mammal of a given size. This measure is hypothesized to be a rough estimate of the intelligence of that animal.

Endosymbiosis A type of **symbiosis** in which one organism (the symbiont) lives in the body of the other organism.

Enzyme A **protein** that functions as a biochemical **catalyst**. Each enzyme is highly specific to the reaction it catalyzes.

Eukaryote An organism that has cells which contain a membrane-bounded **nucleus** and other membranous organelles as well as a **cytoskeleton**.

Europa The fourth largest moon of Jupiter which is believed to have a global subsurface ocean underneath its ice cover. Since that ocean is thought to be in contact with the rocky interior of the moon, **hydrothermal vents** might exist on that interface.

Eusocial A social system in which there is a division of labor into reproductive and non-reproductive groups (e.g., a single female or caste producing the offspring and non-reproductive individuals cooperate in caring for the young) and the presence of overlapping generations within a colony of adults. Eusociality occurs in insects, **crustacean**s, and to some degree in one group of mammals, the mole rats.

EvoDevo Evolutionary developmental biology; the study of the development of an animal from egg to adult in the light of evolution of that animal, and the genes that control development.

Exoplanet Any planet outside of our **Solar System**. As of May 2017 more than 3500 exoplanets have been confirmed to exist.

Facultative Meaning "optional" in a biological sense, for example a facultative aerobic organism can use oxygen to meet its energy needs, but has also other options which do not require oxygen.

Fauna All of the animal life of a particular region or a particular time such as the **Edicaran fauna**.

Fermi Paradox The term usually used for the observation that because of all the planetary real estate that we know is out there, we would expect that there is evidence of extraterrestrial intelligent life, but there is none. Attributed to Enrico Fermi, see also **Great Silence**.

Flagella Whip-like appendages protruding from the cell body of certain **bacteria**, **protozoa**, and **eukaryotic** cells enabling it to swim.

Formamide A molecule with one carbon, one nitrogen, one oxygen and three hydrogen atoms (CH_3NO), which is under Earth environmental conditions a clear liquid, mixes well with water, and has an ammonia-like odor.

Fruiting body Any part of an organism that is specifically dedicated to making seeds or spores that can then be dispersed to form new organisms.

Fungus (pl. fungi) An organism that is **eukaryotic** and **heterotrophic** digesting its food externally rather than ingesting it. Fungi can be unicellular or **multicellular** and include the mushrooms, **yeasts**, and molds.

Gamete An organism's reproductive cells, which are **haploid**. Female gametes are called ova or egg cells, and male gametes are called sperm.

Ganymede The largest moon of Jupiter, which might have a subsurface ocean (like **Europa**) but that ocean would be sandwiched between two ice layers.

Gene Basic physical and functional unit of heredity, highly variable in size (in humans ranging from a few hundred **DNA** bases to more than 2 million). Genes can be 'coding' (meaning that they direct how a protein is made) or 'non-coding' (usually meaning that they are involved in the control of other genes).

Genetic drift Change in the frequency of certain **gene** variants in a population due to chance only, not based on fitness of the organism.

Genetic recombination The production of offspring with a combination of traits that differ from those found in either parent. In **eukaryotes**, **meiosis** is one process in which that can occur.

Genome The collection of every DNA sequence in an organism (other than invading viruses or bacteria).

Genotype The total set of DNA sequences (genes) within an organism that effect what the organism looks like. Note that some DNA in the **genome** may not affect the **genotype**.

Geomagnetic field Earth's magnetic field that extends into space and protects Earth's surface (and **biosphere**) from the solar wind.

Gibbon Apes of the family Hylobatidae and smaller than the **great apes**. They live in tropical and subtropical rainforests.

Gibbs free energy The energy associated with a chemical reaction that can be used to perform useful work.

Glucose A simple sugar with 6 carbon, 6 oxygen, and 12 hydrogen atoms ($C_6H_{12}O_6$), made during **photosynthesis** from water and carbon dioxide. A derivative form (glycogen) is used by animals for energy storage.

Golgi body An organelle of most **eukaryotic** cells involved in intracellular transport consisting of a complex of vesicles and folded membranes within the **cytoplasm**.

Great apes Primates in the family Hominidae, which includes the gorillas, orangutans, chimpanzees, **bonobo**s, and humans.

Great filter A concept originating with Robin Hanson as answer to the **Fermi Paradox**—that there must be some kind of a barrier that restricts the common occurrence of extraterrestrial intelligent and technologically advanced life despite the common occurrence of habitable planets.

Great Oxygenation Event The rapid rise of oxygen in the Earth's **atmosphere** about 2.4 billion years ago, from an atmosphere with essentially no oxygen to one with between 0.1 and 1% oxygen (compared to 21% today). The oxygen was made by **cyanobacteria** using the photosynthetic pathway that produces oxygen as a by-product **(oxygenesis)**.

Great silence A term used to describe the non-detection of signals deriving from extraterrestrial intelligences by **SETI** programs.

Habitable Refers to a range of environmental parameters that are thought to be favorable to the presence of life allowing the organism to **metabolize**, grow, and reproduce.

Habitable zone (HZ) The distance of a planet around its central star, where it is expected to retain liquid water stably on its surface.

Hadean A time period from approximately 4.6 to 4.0 billion years ago, see Box 1.2. Traditionally thought as an unhospitably hot and violent time period during which life could not exist, but this notion has recently been changing. For example, liquid surface oceans might have already existing on the early Earth 4.3 billion years ago.

Hemoglobin An iron-rich protein in red blood cells that carries oxygen from the lungs to the body's tissues in **vertebrates**.

Halobacteria A genus of microorganisms consisting of several species of **archaea** with an **aerobic metabolism** that live and require an environment with a high concentration of salt.

Haploid A cell that has a single set of unpaired **chromosomes**.

Herbivore An animal that feeds on plant material.

Heterotroph An organism that needs organic carbon to grow, which it obtains by consuming other organisms or their remains (compare with **autotroph**).

Histone Highly alkaline **proteins** found in the **nucleus** of **eukaryotic** cells that package and order the **DNA** into structural units.

Horizontal gene transfer Exchange of genetic material not occurring from the parent to the offspring, see Box 4.4.

Hox genes A group of related **gene**s that control the body plan of an organism.

Hydrogenosome A membrane-enclosed organelle, which occurs in some **ciliates**, **fungi**, and animals, to produce energy. Related to, but not the same as, mitochondria.

Hydrogen peroxide A highly oxidizing compound consisting of two hydrogen and two oxygens molecules (H_2O_2).

Hydrogen sulphide A gas consisting of two hydrogen and one sulfur atom (H_2S). It is well-known for its rotten egg smell. Hydrogen sulphide is commonly released by volcanic activity and also might have had a role in the origin of life process on Earth.

Hydrothermal vent A crack or other opening in the ocean floor from which hot, mineral-rich gases exit. In the 1980s it was discovered that a diverse biota exist at many of these hydrothermal vents on Earth. These included not only microbial life, but also **complex life** such as tube worms, sponges, and an occasional octopus.

Insectivore A carnivorous plant or animal that eats primarily insects.

Invertebrate A group of animals that have no vertebral column (backbone). In fact, by far, most animals are invertebrates.

IQ *Intelligence quotient*, a total score derived from one of several standardized tests, typically designed to determine human intelligence. It is controversial how well IQ relates to other measures of intelligence, whether IQ test results can be compared between cultures, or even what intelligence is.

Incisor (teeth) A narrow-edged tooth at the front of the mouth, adapted for cutting and gnawing. Humans have four incisors in each jaw.

Infanticide The killing of young offspring by a mature animal of its own species. Among mammals infanticide is a strategic way for males to ensure that their own offspring survive.

Io The innermost moon of Jupiter and volcanically most active planetary body in our **Solar System**.

Iron-Sulfur-World A hypothesis advanced by Günter Wächtershäuser that life originated at a volcanic hydrothermal vent system involving minerals and metals such as iron and nickel as critical **catalyst**s.

Isotopic fractionation A enrichment of a specific isotope (an isotope of an element is a variant with the same chemical properties but a nucleus containing a different number of neutrons, which can be stable or radioactive). An enrichment of lighter isotopes is in some instances taken as evidence for biology, as the chemistry of how **enzymes** work sometimes mean they process lighter isotopes faster than heavier ones.

Jerboa A hopping desert rodent found throughout Northern Africa and Asia, belonging to the family Dipodidae.

Jurassic A time period from approximately 201 to 145 million years ago, see Box 1.2.

Kinetics (in a chemical sense) The speed a chemical reaction is proceeding, see also Box 4.1.

Last common ancestor (LCA) The organism that is thought to be the ancestor of all life on Earth—also referred to as Last Universal Ancestor (LUA) or Last Universal Common Ancestor (LUCA).

Late heavy bombardment An inferred increase in large impacts of asteroids or comets on Earth between 4.1 and 3.8 billion years ago based on frequencies of impact craters on the Moon. It is still unclear if there was an increase in such impacts, or whether this was just the tail end of the accretion of the Solar System.

Lichen An organism formed by a symbiotic relationship between a **fungus** and an **alga**e or **cyanobacteria**, or both.

Loricifera A **phylum** of small animals dwelling in marine sediments that have a protective outer case (lorica). Three species have been recovered from the bottom of the Mediterranean Sea and it has been suggested that they have an oxygen-free environment as their habitat, capable to do so because of having **hydrogenosome**s instead of **mitochondria**, but that is controversial.

Macrofauna Animals that are at least one centimeter in size, in some applications understood as **invertebrates** that live in or on the seafloor sediment.

Macromolecule A molecule containing a large number of atoms, usually understood to be size of a **protein** or a **nucleic acid** such as **DNA**.

Magpie A bird of the **Corvidae** family, which is quite intelligent and able to recognize itself in the mirror test.

Main sequence star A star that generates light and heat by the conversion of hydrogen to helium through nuclear fusion in its core. Most stars are main sequence stars, as is our Sun. "Main sequence" refers to the relationship between mass and temperature that defines both Main Sequence stars' brightness and their lifetime.

Many Path Model Model used in this book to describe how a key innovation in function can be provided by many different structures (chemical or anatomical), and hence can occur in many different ways in different organisms.

Meiosis A cell division which leads to **gamete** formation and in which the **chromosomes** are reduced from **diploid** to **haploid**.

Melanin A dark brown to black **pigment**, which occurs in the hair, skin, and iris of the eye in humans and many animals, and is also responsible in humans for the tanning of the skin after **UV** exposure.

Metabolism The totality of biochemical processes by which energy from an external environment is utilized by the organism to maintain its internal order and to execute all its other functions such as growth and reproduction.

Metabolite Intermediate product or end product of **metabolism**; the term is usually used for smaller molecules such as **glucose** or **amino acids**.

mRNA messenger RNA, a large family of **RNA** molecules that convey genetic information from **DNA** to the **ribosome**.

Methane A compound with one carbon and four hydrogen atoms (CH_4), which is a colorless gas under Earth surface temperatures. On Saturn's moon **Titan** methane is a component of the hydrocarbon lakes existing on Titan's surface.

METI Abbreviation for Messaging to ExtraTerrestrial Intelligence, also known as active **SETI**. The activity (proposed or conducted) of sending messages out into space to contact intelligent extraterrestrial life.

Microbialite Structures formed of biological material and sediments by microbes binding and trapping sediment particles.

Microsporidia **Eukaryotic**, unicellular organisms of the **phylum** Microspora, which are **obligate**, **spore**-forming, intracellular **parasite**s of both **vertebrates** and **invertebrate**s.

Mimicry The action or art of imitating someone or some other animal.

Mimosa A perennial herb that is sensitive to touch; when touched, it folds inward defending itself from harm, but opens a few minutes later.

Mitochondria Organelles in the **cytoplasm** of **eukaryotic** cells with the main function of producing energy. Mitochondria have their own DNA and are thought to have evolved by **endosymbiosis**.

Mitosis The process of **diploid** cell division with the result of two daughter cells that are identical to each other and their parent cell.

Mollusc Mostly marine **phylum** of many **invertebrate** organisms to which snails, mussels, but also the **cephalopod**s belong.

Monomer A molecule that can be linked with identical or different molecules to form **polymer**s.

Multicellular An organism composed of a minimum of two different cell types.

Muscle A soft tissue in most animals containing **protein** filaments that can produce a contraction changing the length and shape of a cell, critical for many organism to achieve motion.

Mutation A change in the **DNA** of a cell that happens as a single event. A mutation can be the loss or duplication of a whole **gene**, a change in the **nucleotide** sequence, an alternation in **gene** position, or an insertion of foreign **nucleotide** sequences (for example, by a virus).

Mycorrhiza A symbiotic relationship between the roots of a **vascular plant** and a **fungus**.

Myxobacteria Also known as slime bacteria. Myxobacteria are rod-shaped bacteria that are nearly ubiquitous in Earth's **biosphere**. They have very large genomes compared to other bacteria (9–10 million **nucleotides**) and produce **fruiting bodies** in starvation conditions.

Neanderthal *Homo neanderthalensis*, a human species or subspecies of the genus Homo. Neanderthals became extinct around 40,000 years ago. They had 99.7% of the same **DNA** as modern humans and also had a slightly larger brain, although their intelligence compared to modern humans is unknown.

Nematode Worms of the **phylum** Nematoda, also called roundworms. They are typically approximately 5–100 micrometer thick, and at least 0.1 millimeter long, They occur in diverse environments including extreme environments such as Antarctica, but also as parasites.

Nematocyst An explosive cell containing one giant secretory organelle occurring in the **phylum** of the Cnidaria (corals, sea anemones, hydrae, jellyfish, etc) that causes a sting.

Neolithic The later part of the Stone Age, between about 10,200 BC and 4500–2000 BC, when ground or polished stone weapons were common.

Neuron A cell that processes and transmits information through electrical and chemical signals. Neurons are the primary components of the brain, but also the entire nervous system. These are called 'excitable' cells because they can produce a pulse of electric current on being 'excited' by a specific chemical or electrical signal.

Nucleariids A group of **amoeba** that are usually small, up to about 50 micrometer in size belonging to the genus of the *Nuclearia*.

Nucleic acid Polymers that consist of **monomer**s known as **nucleotides** and can carry information. **DNA** and **RNA** are nucleic acids.

Nucleotide Basic structural unit (**monomer**) of a nucleic acid such as **DNA**.

Nucleoid The region within a **prokaryotic** cell that contains all or most of the genetic material. Similar to the **nucleus** in **eukaryote**s, but not surrounded by a membrane.

Nucleus (biology) A membrane-bound **organelle** that houses the **chromosomal DNA** in a **eukaryotic** cell. Only **eukaryotic** organisms have a **nucleus**.

Obligate Restricted to a particular function or mode of life, e.g. an obligate multicellular organisms is bound to its multicellular state, and cannot revert back to a single-cellular state.

Omnivore An organism that meets its energy and nutrient requirements from a diet consisting of both animal tissue and plant material.

Opossum A marsupial mammal of the order Didelphimorphia, common in South and North America.

Orca A toothed whale, largest member of the oceanic dolphin family, known as intelligent predator, hunts large prey animals such as seals. Used to be (inaccurately) known as 'killer whales'.

Organelle A subsection within a cell, bound by a membrane, that carries out a specific function. Examples include the **nucleus**, **mitochondrion**, and **golgi apparatus**.

Ordovician A time period from approximately 488 to 444 million years ago, see Box 1.2.

Ostracod Small **crustacean**s, varying from 0.2 to 30 millimeter in size and belonging to the class Ostracoda.

Oxygenesis The production of oxygen by **photosynthetic bacteria** such as **cyanobacteria** and by green plants and algae that contain **chloroplasts**.

Ozone layer A layer in the stratosphere of the triatomic form of oxygen (O_3) which efficiently filters out **UV radiation** from the Sun. The **ozone layer** means that UV-sensitive life can live at the Earth's surface, including on land.

Parasite An organism that lives in or on another organism and benefits from it by deriving nutrients, harming the host organism.

Peptide bond Chemical bond that links **amino acid**s together to form **proteins**. Forming a peptide bond is a condensation reaction, i.e. one that forms a water molecule as a product of the reaction.

Peptide nucleic acid An artificially synthesized **polyme**r similar to **DNA** or **RNA**.

Permian A time period from approximately 299 to 252 million years ago, see Box 1.2.

Phagocytosis The process by which a cell takes in particles such as **bacteria**, **parasite**s, dead host cells, or cellular and foreign debris. The cell engulfs the particle in a membrane-bounded sack formed from its outer cell membrane. Phagocytosis can be done by a free-living unicellular organism, such as a **protozoa**, and also by certain cells of animals such as white blood cells.

Phenotype Physical characteristics of an organism, programmed by the **gene**s.

Photoautotroph An organism that synthesizes all the organic compounds it needs from inorganic chemicals and light as an external energy source.

Photon The fundamental particle of electromagnetic radiation, such as light, X-rays and radio waves.

Photosynthesis A process used by a variety of organisms including plants to convert light energy into chemical energy (e.g. carbohydrates).

Phylum (*plural phyla*) A taxonomic category that ranks below kingdom, but above class. Examples of kingdoms are Animals and Plants. Examples of phyla are chordates (everything with a backbone-like structure) or **arthropods**, examples of classes are Mammals or Insects.

Physiology An area of biology dealing with the functions and activities of living organisms and their parts. In modern times, 'physiology' has generally meant the way that chemical and biochemical systems support the functions of the body, although physical processes (such as breathing) and anatomy are important aspects of this.

Phytol A chemical compound needed to assemble **chlorophyll** and consisting of 20 carbon atoms, 40 hydrogen atoms and one oxygen atom ($C_{20}H_{40}O$).

Picoplankton Fraction of plankton composed by cells between 0.2 and 2 micrometer in size.

Pigment A compound that changes the color of reflected or transmitted light as the result of absorption that is dependent on the wavelength of that light.

piRNA Piwi-interacting RNA, the largest class of small non-coding **RNA** molecules expressed in animal cells.

Piwi protein A group of proteins involved in gene control in many eukaryotes.

Placenta An organ in mammals connecting the developing fetus to the wall of the uterus. It provides oxygen and nutrients to the growing embryo and removes waste products from the embryo's blood.

Plankton Small and microscopic organisms drifting or floating typically in the oceans but also in fresh water. Plankton primarily consists of small **crustacean**s, **diatom**s, **protozoa**ns, and the eggs and larval stages of larger animals.

Planetesimal An object in space formed from dust, rock, and other materials by **accretion**, an intermediate in forming planets. Typically they are postulated to be several meters to hundreds of kilometers in diameter.

Plastid A double-membrane organelle occurring in plants (e.g. **chloroplast**) and certain **protist**s such as **algae** containing **ribosome**s, **prokaryotic DNA**, and often **pigment**.

Plate tectonics The movement of crustal plates near the surface of a planet or large moon, which is typically driven by the heat of radioactive decay occurring inside the planet. Very important for long-term **habitability** due to its effect on nutrient cycling and stabilizing the climate.

Platypus A semiaquatic egg-laying mammal of eastern Australia, often called 'Duck-billed platypus, because of its bill and the bill's similarity to the bill of a duck.

Pluto A dwarf planet beyond the orbit of Neptune. Also, besides the Earth-Moon system, Pluto is the only known planet part of a double planet system, with its moon Charon being relatively large compared to Pluto.

Polymer A large molecule, or **macromolecule**, composed of many **monomer**s or repeated subunits.

Porpoise A group of marine mammals that are very closely related to oceanic dolphins.

Primate Any member of the group of animals that includes humans, apes, and monkeys.

Prokaryote A microbial organism that does not possess a distinct **nucleus** or other membrane-bound specialized organelles. Both **archaea** and **bacteria** are prokaryotes.

Proteorhodopsin A family of over 50 **protein**s that are able to harvest the energy of light, often used by marine **bacteria**.

Proterozoic A time period from approximately 2.5 billion years ago to about 542 million years ago, see Box 1.2.

Protist Any **eukaryotic** organism that is not an animal, plant or **fungus**.

Protoplanet A large body of matter in orbit around a star (such as our Sun) thought to be developing into a planet. Protoplanets are believed to be formed by **accretion** of **planetesimals** and gas or dust in a disc orbiting new stars.

Protozoa A diverse group of unicellular **eukaryotic** organisms that are mobile and eat other microscopic organisms, and so mirror animal behavior to some degree. A subkingdom of the kingdom Protista.

Proxima b An exoplanet orbiting within the **habitable zone** of the red dwarf star **Proxima Centauri**, but unlikely to be **habitable**.

Proxima Centauri A red dwarf star, which is at a distance of 4.24 light years nearest to the Sun. It is probably part of the **Alpha Centauri** system. Its flares and emits **X-rays** and high-energy **UV radiation**, thus would challenge the habitability of any orbiting planets such as **Proxima b**.

Psittaciformes A group of birds that includes the parrots and live in subtropical and tropical regions. They live in families, groups, or flocks, and have developed excellent communications skills.

Pterosaur Flying reptiles of the extinct order Pterosauria. They existed from the late **Triassic** to the end of the **Cretaceous** (228–66 million years ago).

Pulling-up-the-Ladder event The circumstance when an evolutionary innovation destroys the preconditions for its own occurrence.

Random Walk model The hypothesized model of evolutionary innovation in which a key innovation is up to chance and highly unlikely, because it requires a highly improbable event to occur, or a number of highly improbably steps. Different from the **Many Paths** model because the **Random Walk model** requires a specific set of events to occur in the right order.

Rare Earth (hypothesis) A hypothesis suggesting that the origin of life and the evolution of biological complexity toward technological intelligence requires an improbable combination of astrophysical and geological events and circumstances, thus complex extraterrestrial life (and a truly Earth-like planet) would be exceedingly rare.

Reactant A substance that undergoes change during a chemical reaction.

Reactive Oxygen Species (ROS) Chemically reactive compounds of oxygen, such as **hydrogen peroxide**.

Red dwarf A small, dim **main-sequence star** of 0.1–0.5 solar masses and a surface temperature range of 2500–3500 °C, also referred to as dM star (but can also be a late dK star).

Red edge See **Vegetation Red Edge**.

Rhodopsin A pigment found in the rods of the retina, which is extremely sensitive to light, and thus enables vision in low-light conditions. *Rhodopsin* is found in a wide range of organisms, from **vertebrate**s to **bacteria**.

Ribonucleic acid (RNA) A **nucleic acid** present in all cells and organisms of life as we know it. Its primary role is to carry instructions from **DNA** for controlling the synthesis of **protein**s. However, in some viruses **RNA** rather than **DNA** carries the genetic information and during the origin of life phase it may have had this role and others (e.g. as **catalyst**) as well.

Ribonucleic acid (RNA) world A stage in the appearance of life that has been hypothesized to exist prior to the evolution of **ribosomes** and **DNA** where **RNA** took both the role as molecule to transmit information from one generation to the other and as a **catalyst**.

Ribosome A cell organelle in **prokaryotes** and **eukaryotes** that serves as the site of biological **protein** synthesis and which consists of **RNA** and associated **protein**s. Ribosomes are found in large numbers in the **cytoplasm** of cells.

Rotifer Microscopic typically aquatic animals of the **phylum** Rotifera. Rotifers are so named because of the wave-like movement of cilia (tiny hair-like structures) at the front end making it look like they are rotating on a wheel.

RuBisCo A key **enzyme** involved in the process by which atmospheric carbon dioxide is converted by plants and other photosynthetic organisms to energy-rich molecules such as **glucose. RuBisCo** adds carbon dioxide into a sugar molecule, generating two smaller, new sugars.

SETI Abbreviation for The Search for Extraterrestrial Intelligence (***SETI***), a collective term for the scientific search for intelligent extraterrestrial technological civilizations, which is directed to some part by the SETI-Institute (http://www.seti.org/).

Shadow biosphere A hypothesized microbial biosphere existing on Earth that is markedly different in biochemistry and molecular processes from life as we know it. It might have gone unnoticed, because the standard way of discovering new life is to characterize its **DNA**; if the shadow biosphere does not use DNA, it would not be detected by these methods.

Shellfish Aquatic **invertebrate**s with an exoskeleton, which includes various species of **mollusc**s and **crustacean**s. Shellfish are often used for human consumption.

Silurian A time period from approximately 443 to 416 million years ago, see Box 1.2.

Slime mold A group of **eukaryotic** organisms that can live freely as single cells, but aggregate together to form **multicellular** reproductive structures. The life cycles of slime molds typically includes a phase in which they appear as gelatinous slime. They generally feed on microbes that live in dead plant material.

Snowball Earth An event when Earth's surface was largely or almost completely covered with ice, including the surface of the oceans. There were at least two time periods when this event happened (independently), 2.3 billion years ago and between 730 and 580 million years ago.

Solar system All planets, moons, dwarf planets, comets, asteroids, and dust and gas orbiting a star (including our Sun).

Solvent A liquid in which some other chemical compound is dissolved to form a solution. On Earth water is the solvent universally used by life, but other solvents are in principle possible as the basis for life on other planets and moons such as ammonia or methane.

Soma All cells of an animal or a plant except the reproductive cells (germ cells).

Spore Resistant structures used by many **bacteria**, plants, **alga**e, **fungi** and **protozoa** for survival under unfavorable environmental conditions, but also used for dispersal.

Spreading zone An area, where Earth's continental or oceanic plates move apart. Typical are mid-ocean spreading zones, where new crust is created by magma welling up from the mantle and the oceanic plates on both sides move apart in opposite direction.

Starshade A screen that can open like a set of flower petals suggested to be used in a future space mission in front of a telescope to block the star's light, so as to better observe the planets around that star.

Stromatolite Layered rocks of limestone created by **bacterial mats** (especially colony-forming **cyanobacteria**) that form in shallow water by the trapping, binding and cementation of sedimentary grains. Fossilized stromatolites provide some of the oldest records of life on Earth, dating back to more than 3.5 billion years ago.

Sunglint The glint or flash of light when sunlight reflects off the surface of a large body of liquid at the same angle that a satellite or other sensor is viewing the surface. Also called specular (mirror-like) reflection.

Supervolcano A volcano that is capable of producing a volcanic eruption with an ejecta mass greater than 1 trillion tons.

Surfactant A chemical compound that reduces the surface tension of a liquid in which it is dissolved. Soaps and detergents are surfactants.

Swarm intelligence The collective behavior of decentralized, self-organized systems, which can be natural such as a bee hive or artificial such as cellular robotic systems.

Symbiosis The close and often long-term physical interaction between two different biological species with advantages to both species.

Symbiont Either of the two organisms of a different species that live in **symbiosis** with one another.

Tar A dark mixture of many hydrocarbon and other carbon compounds, often consisting of a large proportion of very large, very complicated molecules whose exact structure is hard to determine.

Tardigrade A microscopic animal which is extremely resistant to environmental stresses, such as temperature, radiation, and lack of water, especially in its **tun** state. Also sometimes called 'water bears' or 'moss piglets', the latter because they live in the water around moss (among many other places).

Tendon A tough band of fibrous connective tissue. It usually connects muscle tissue to a bone and is capable of withstanding a high degree of tension.

Tenrec A mammal of the family Tenrecidae, similar to shrews and hedgehogs and found on Madagascar and in parts of the Africa.

Teleomere A region of the **DNA** sequence at each end of a **chromosome**, which protects the end of the **chromosome** from deterioration and from fusion with neighboring **chromosome**s.

Tertiary A time period from approximately 65 to 2.6 million years ago, see Box 1.2.

Tidal flat Non-vegetated, soft sediment and muddy surfaces that are alternately submerged and exposed to the air by changing tidal levels.

Tidal flexing When a body is pulled by tides (the gravitational effect of another, nearby planet or star), so that it changes shape slightly. Tidal flexing can release substantial energy inside a planet or moon as its rocks are stretched and compressed. Tidal flexing is thought to be at least in part the cause of a subsurface ocean at **Europa**, a moon of Jupiter.

Tidal locking When the orbital period of a planetary body matches its rotational period. As a result a moon may always show the same face to the planet it orbits (like our Moon) or a planet may always show the same face to the star it orbits.

Titan The largest moon of Saturn with an **atmosphere** of 1.5 bar (1.5 times the surface pressure of Earth). Titan is the only other planetary body in our **Solar System** with stable liquids on its surface, in form of hydrocarbon lakes.

Thermodynamic disequilibrium State when a system of chemicals could react so as to release energy. They may react, or may be kinetically inhibited from reacting. See also Box 4.1.

Thermodynamics A branch of science dealing with heat and temperature and their relation to energy and work, governed by the laws of *thermodynamics.*

Thermophile An organism that lives at relatively high temperatures, above 41 °C. The current temperature record is at 122 °C. Organisms that live at the upper end of this scale (>90 °C) are also referred to as hyperthermophiles.

Transcription (genetic) The first step of **gene** expression involving a segment of **DNA** being copied into **RNA** with the help of an **enzyme** (RNA polymerase).

Translation The second step in **gene** expression, where the sequence of a molecule of **RNA** is used to direct linking **amino acids** in a specific order into a **protein**, and carried out on **ribosomes**.

Triassic A time period from approximately 251 to 199 million years ago, see Box 1.2.

Trilobite A group of marine arthropods that has been extinct since the **Permian** time period.

Triton The largest moon of the planet Neptune with a diameter of 2700 kilometer and thought to have been a dwarf planet which was captured by Neptune's gravity.

tRNA transfer **RNA**, typically 76–90 **nucleotides** in length, that helps decode a **mRNA** sequence into an **amino acid** sequence of a **protein** during the process of **translation**.

Troodon A genus of bird-like theropod dinosaur with some of the highest **encephalization quotients** among dinosaurs.

Tun A dormant, resistant state of **tardigrades** (water bears) to cope with environmental extremes such as freezing temperatures.

Ultraviolet (UV) radiation That part of the Sun's radiation with a wavelength between 400 and 10 nanometer, lying in the electromagnetic spectrum between visible light and **X-rays**.

Variance A measure of how far a set of numbers are spread out from their mean, calculated by the expected value of the squared deviation of a random variable from its mean.

Vascular plant Higher land plants that have specialized tissue for conducting water and minerals throughout the plant. Trees and grasses are examples of vascular plants, mosses are not.

Vegetation red edge Region of rapid change in reflectance of vegetation in the near infrared range of the electromagnetic spectrum due to the **absorbance spectrum** of **chlorophyll** and other plant pigments and scattering due to the leaves' internal structure.

Vegetative cell A cell of a **bacterium** or unicellular **alga** that is actively growing rather than being in a **spore** state or forming **spore**s.

Venus flytrap A **carnivorous** plant indigenous to the subtropical wetlands on the East Coast of the United States.

Vertebrate Animals with an internal skeleton, specifically including a backbone, of the subphylum Vertebrata and the **phylum** Chordata, which include fish, amphibians, reptiles, birds, and mammals.

Viviparity Giving birth to living young that develop within the mother's body rather than hatching from eggs. Most mammals and some other animals are viviparous.

Xanthophyll A yellow pigment that is common in nature and occurs, for example, in leaves.

X-ray A form of high energy electromagnetic radiation with a wavelength ranging from 0.01 to 10 nanometer.

Yeast A unicellular **eukaryotic** organism belonging to the kingdom of the **fungi**. Brewers' and bakers' yeasts are one species of yeast, but there are many others.

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